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[With Five Plates, illustrating Dr. A. E. Trueman's Paper.]

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SESSION 1919–1920.

1919.

Wednesday, December ..... 3 —17*

1920.

Wednesday, January ..... 7*—21*
„ February (*Anniversary Meeting*, Friday, February 20th) . 4*—25*
„ March ..... 10—24*
„ April 21*
„ May ..... 5 —19*
„ June ..... 9 —23*

[*Business will commence at 5.30 p.m. precisely.*]

The asterisks denote the dates on which the Council will meet.

10. *The* Evolution *of the* Liparoceratidæ. By Arthur Elijah Trueman, D.Sc., F.G.S., University College of South Wales and Monmouthshire, Cardiff. (Read April 17th, 1918.)

[Plates XXI–XXV.]

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I. Introduction.

The ammonites dealt with in this paper are characteristic of the uppermost zones of the Lower Lias (Charmouthian), and they are of three general types, namely:—

(1) A capricorn form, evolute slender whorls (serpenticone) with stout simple ribs.
(2) An involute form with swollen whorls (sphærocone), bituberculate, generally known as *A. striatus* or *A. bechei*.
(3) A form intermediate between these two, with capricorn inner whorls, the outer whorl swollen, with more numerous slender ribs bearing two rows of tubercles (usually known as *A. heterogenes*).

In order to name some ammonites collected at Lincoln, apparently similar to those called *A. striatus*, the relationships of these types were studied; it presently became clear that the classification of these ammonites, and the correlation of the beds in which they occur, needed to be considerably revised, and that such a revision must be preceded by an investigation of all available ammonites composing the family Liparoceratidæ. With this in view, a large number of these fossils was collected from practically all the English exposures, their precise horizons were noted, and developmental and sutural evidence was examined. The present paper includes the main results of this work. Several new specific names are proposed, but only where this is necessary to define a series: future work may show that many of the intermediate forms mentioned must also receive separate names, but, as this paper is mainly concerned with establishing the lineages and their geological ranges, minute description of species has not been undertaken.

In the course of this investigation much assistance has been received from other workers. Dr. W. D. Lang kindly placed at

my disposal his carefully collected material from the Dorset cliffs, while other specimens have been lent by Mr. S. S. Buckman, Mr. L. Richardson, Mr. J. W. Tutcher, and Mr. C. H. Watson.

Mr. C. P. Chatwin directed my attention to the Napton (Warwickshire) exposure, and this led to the discovery of an important series of ammonites.

For permission to examine material, and for assistance while working in the various museums, I am indebted to Mr. G. W. Lamplugh and Mr. H. A. Allen (Jermyn Street Museum), Dr. A. Smith Woodward and the late Mr. G. C. Crick (British Museum—Natural History), Mr. E. E. Lowe (Leicester), Mr. A. Smith (Lincoln), Prof. J. W. Carr (Nottingham), Mr. T. Woodhouse Parkinson (Whitby), Mr. S. E. Harrison (Cheltenham), and Mr. H. Woods (Sedgwick Museum, Cambridge).

In the field, help has been given by Mr. W. E. Howarth (in Lincolnshire and Yorkshire), by Mr. J. T. Sewell (Whitby), Mr. J. W. Gray (Cheltenham), and Mr. C. H. Watson (Napton).

Prof. T. F. Sibly kindly read my manuscript, and offered various suggestions; while Prof. G. Norwood and Mr. C. Brett have helped with the nomenclature.

My special thanks are due to Prof. H. H. Swinnerton for his continued advice and encouragement, and to Mr. S. S. Buckman for the help that he has so readily given in numerous ways.

II. Historical Notes.

Early in the last century Sowerby figured two ammonites which he called *Ammonites henleyi* and *A. bechei*, while Reinecke described a somewhat similar form as *A. striatus*. While these species are in themselves quite distinct when fully understood, there are so many apparently intermediate stages that it is not surprising that confusion quickly arose in the use of the names.

Thus A. d'Orbigny's *A. henleyi* (3,[1] pl. lxxxiii) is an ammonite which I consider to be closely related to those forms that have been called *A. striatus* Reinecke, while *A. henleyi* Reynès[2] is unlike any English fossil that I have seen. Similarly, a number of the specimens figured by Quenstedt (4, pl. xxix) are allied to *A. nautiliformis* J. Buckman, a member of quite a different series.

The naming of the capricorn ammonites presented similar difficulties: for, until the different species are closely compared, they appear to be very similar. The three best-known species are *A. capricornus* Schlotheim, *A. latæcosta* Sowerby, and *A. maculatus* Young & Bird; the first name has been most frequently used. E. F. Schlotheim[3] in describing this species gave no figure,

[1] These numbers in parentheses refer to the List of Literature, § VIII, p. 293.

[2] P. Reynès, 'Essai de Géologie & de Paléontologie Aveyronnaises' 1868, p. 88 & pl. i, figs. 2*a*–2*b*. Compare *Ægoceras spoliatum*, K. Futterer, 'Die Ammoniten des Mittleren Lias von Œstringen' Mitt. Bad. Geol. Landesanst. vol. ii (1893) pl. x, fig. 1.

[3] 'Die Petrefactenkunde' 1820, p. 71.

and, although Schlœnbach has more recently studied the type-specimens,[1] it is still uncertain precisely which species is covered by the name *A. capricornus*, and for the present it is perhaps better not to use the name. When the name *A. maculatus* has been employed it has nearly always been misapplied, as, for example, by Wright and Quenstedt; while the term *A. latæcosta*, which covers a species that is related to many of our English capricorns, has until lately been very little used.

All the above-mentioned writers, while they often figured sutures of these ammonites, made no use of the suture as a means of identification. F. von Hauer,[2] who described another capricorn in 1854, pointed out the features in its suture by which it might be distinguished from the ammonites that it resembled. Apparently his remarks have hitherto been overlooked.

In 1867 Hyatt proposed the three genera *Microceras*, *Androgynoceras*, and *Liparoceras*, to include respectively the capricorn ammonites, the ammonites of the *heterogenes*-type, and those of the *striatus*-type. Such an arrangement made generic identification simple, since each genus was comparatively distinct. Wright concluded, however, from a study of these fossils, that *A. henleyi* was descended from a capricorn form, *A. latæcosta*, and similarly that *A. heterogenes* had inner whorls resembling those of *A. capricornus* (8, p. 370). That is to say, Wright recognized two genetic series, each of which included capricorn and *heterogenes*-like forms. While Wright also noted that the outer whorl of *A. heterogenes* resembled *A. striatus*, he did not suggest that this latter ammonite was a further advance along the same line of descent, because the inner whorls of *A. striatus* show no trace of capricorn ornamentation. E. Haug[3] also noticed the smooth inner whorls of *A. striatus*, and suggested that they resembled *A. globosus*; still more recently Prof. J. Perrin Smith has included *A. bechei* and similar species with the Polymorphinæ, separating them from the remainder of the Liparoceratidæ, presumably for the same reason.[4]

Mr. S. S. Buckman suggested, however, in 1891,[5] that ammonites of the *A.-striatus* type are descended from capricorn ammonites, the capricorn style of ornamentation being omitted in the development of advanced members of the series as the quickest method of producing shells of globose form. This conclusion is supported by the details to be given later. Mr. Buckman accordingly revised

[1] Schlœnbach studied Schlotheim's type-specimens of *A. capricornus*, and said that they were identical with *A. maculatus* Quenstedt. See U. Schlœnbach, 'Ueber den Eisenstein des Mittleren Lias, &c.' Zeitschr. Deutsch. Geol. Gesellsch. vol. xv (1863) p. 465; but this is not sufficiently definite to be of value.

[2] 'Beiträge zur Kenntniss der Capricornier der Œsterreichischen Alpen' Sitzungsb. K. Akad. Wissensch. Wien, vol. xiii (1854) p. 94.

[3] 'Ueber die Polymorphidæ, &c.' Neues Jahrb. vol. ii (1887) p. 103.

[4] J. P. Smith in Eastman-Zittel, 'Text-book of Palæontology' 2nd ed. vol. i (1912) p. 67.

[5] S. S. Buckman, 'Monograph of the Inferior Oolite Ammonites' Palæont. Soc. p. 289 (footnote).

Hyatt's genera to express this interpretation, and limited each generic name to a series which evolves from capricorn to bituberculate sphærocone (1, vol. i, p. *iii*). That is to say, those generic names which were formerly applied to morphic equivalents on several lineages were made to include the heteromorphic stages of phylogenetic series. *Microceras* was applied to an earlier series, while *Androgynoceras* and *Liparoceras* were limited to series of those ammonites that have respectively elevated and depressed whorls. At a later date A. Hyatt[1] used the name *Amblycoceras* to include certain capricorns; the specimen then figured is peculiar in having costæ with a slight peripheral curve, and Mr. Buckman proposes to restrict the name for such a series.[2] *Oistoceras* was suggested for capricorns in which the ribs have a very distinct bend on the periphery, more marked than that shown by *Amblycoceras* (1, vol. i, p. *iv*).

Recognizing that there exists at least another series of ammonites passing through comparable stages, Mr. Buckman used Waagen's name *Ægoceras*[3] to indicate them, including here *A. nautiliformis* J. Buckman, which had frequently been confused with *A. bechei*, but from this it is separated by a very considerable time-interval (1, vol. i, p. *iii*).

Summarizing, then, the existing classification of these ammonites, we find the following genera in use:

Liparoceras—Depressed forms with coarse ornamentation.
Genotype selected by Mr. Buckman: *A. striatus* Bronn, *non* Reinecke.

Androgynoceras—Elevated whorl, finer ornamentation.
Employed to include *A. maculatus* Young & Bird, *A. heterogenes* Young & Bird, *A. bechei* Sowerby, *A. henleyi* Sowerby, and many English capricorns.
Genotype selected by Mr. Buckman: *A. hybrida* A. d'Orbigny.

Amblycoceras—Capricorns only hitherto described, with slight peripheral rib-curve. Not otherwise defined.

Oistoceras—A series with marked rib-curve on the venter.
Genotype, *A. figulinus* Simpson. Capricorn stage only known.

Ægoceras—Includes capricorns believed to lead to *A. nautiliformis* J. Buckman.
Genotype, *Ammonites planicosta* (=*capricornus*) A. d'Orbigny.

In constructing the above-named genera little attention has been paid to any characters, except whorl-shape and ornamentation; the sutures have not been compared, and the less obvious details of ontogeny have not been examined. Thus the characters hitherto described are not sufficient to identify a single genus with any certainty; indeed, the species referred to certain genera are in no

[1] In Eastman-Zittel, 'Text-book of Palæontology' 1st ed. vol. i (1900) p. 578.

[2] S. S. Buckman in 'Geology of the Country between Whitby & Scarborough' Mem. Geol. Surv. 2nd ed. (1915) p. 95.

[3] W. Waagen, 'Die Formenreihe des *Ammonites subradiatus*' 1869, p. 247.

way related. It is, therefore, necessary to revise the generic classification.

Each genus, as has been shown, includes ammonites of very different appearance, ranging from capricorn evolute forms to bituberculate involute forms; in constructing the revised classification offered here, the affinities of the various members of the genera have been ascertained by the establishment of continuous series of forms only separated by small differences attributable to accelerated development. Further, the sutures of each of these series have a number of features in common, and these constitute the readiest means of identification.

III. Stratigraphical Notes.

The time-ranges of these ammonite lineages are of importance to the stratigraphical geologist, for the ammonites of this group are dominant in the upper part of the Lower Lias, where it has been usual to recognize a *capricornus* zone overlying a *henleyi* or *striatus* zone. But it is quite clear that the *striatus*-like forms are descended from capricorn ammonites, and such a conclusion can only be reconciled with the facts of stratigraphy by supposing that there were below the *striatus* zone capricorns which gave rise to the involute forms of that horizon, and it is also probable that involute forms have evolved from the capricorns of the *capricornus* zone. Such capricorns of pre-*striatus* age, and involute forms of post-*capricornus* age, will be described from Napton (Warwickshire) and Lincoln respectively.

Until late years it has been supposed that almost all the *striatus*-like forms occurred in the so-called '*striatus* zone.' Recently, however, Dr. W. D. Lang[1] has carefully collected Liassic ammonites in the cliffs of Dorset with reference to their precise position. From a study of his specimens it appears that these forms occur at several distinct horizons, as follows :—

margaritatus zone.		Involute ammonites (of the ? *A. nautiliformis* group).
davœi zone.	*Oistoceras* sub-zone.	Capricorn ammonites (*Oistoceras*) and involute ammonites similar to *A. bechei*.
	Liparoceras sub-zone.	Involute ammonites similar to *A. henleyi*.
	latæcosta sub-zone.	Capricorn ammonites of the *A. latæcosta* group.
ibex zone.		Capricorn ammonites of the *Beaniceras* series (see p. 268). Involute ammonites of the *Liparoceras* series.

It will be noticed that involute ammonites of the *Liparoceras* series are only to be found in the upper part of the *ibex* zone,

[1] 'The Geology of the Charmouth Cliffs, &c.' Proc. Geol. Assoc. vol. xxv (1914) p. 293; 'The *Ibex* Zone at Charmouth, &c.' *ibid.* vol. xxviii (1917) p. 31.

while involute forms of the *henleyi* and *bechei* series occur respectively in the *Liparoceras*[1] and *Oistoceras* sub-zones of the zone of *Deroceras davœi*.

Around Cheltenham, beds with *striatus*-like forms are succeeded by beds with capricorns, these being immediately below the Middle Lias (Marlstone Series) of the district, and this has been accepted as the normal sequence. The *striatus*-like ammonites, however, are of the *Liparoceras* series, and are similar to those found in the upper part of the *ibex* zone of Dorset. Since no higher horizon with involute Liparoceratids has been detected in South Gloucestershire, it is extremely probable that most of the *davœi* zone is not represented there. Further, some of the capricorn ammonites of the Cheltenham district are similar to those found in the *latæcosta* sub-zone of Dorset, while others are of a different type, and probably indicate a horizon that is not represented in Dorset.[2]

At Napton-on-the-Hill (Warwickshire), at Dumbleton, and in some other parts of Gloucestershire, lower beds are present, containing capricorn ammonites of the *Liparoceras* series, of which involute forms only are known in Dorset. As the Napton pit was not in work at the time of my visits no thicknesses can, with any certainty, be assigned to these beds. The following general succession was determined :—

margaritatus zone.	Middle Lias.
latæcosta sub-zone.	Beds with capricorn ammonites of the *A. latæcosta* group.
ibex zone.	Beds with capricorn ammonites of another series (*Beaniceras*).
	Beds with involute *Liparoceras* (*L. obtusinodum* and other spp.).
	Beds with capricorns of the *Liparoceras* series.
	Beds with *Acanthopleuroceras valdani*.
	Beds with *Tragophylloceras ibex*.

The succession at Dumbleton is probably very similar (see Table I). At Radstock (Somerset) bituberculate sphærocones of a different type occur at a still lower horizon: namely, the *valdani* zone, and it is therefore probable that another group of capricorns will be found below this level.

South of Lincoln the upper part of the Lower Lias is again exposed, and the *Oistoceras* and *dædalicosta* sub-zones, which are presumably absent in Gloucestershire and Warwickshire, are represented by thin but very fossiliferous deposits. Fossils of the *Oistoceras* sub-zone may also be found in the lowest beds of the

[1] This is an unfortunate name, since by *Liparoceras* were meant involute ammonites of the *henleyi* series, which are here assigned to *Androgynoceras*, while *Liparoceras* is confined to lower beds. The name *dædalicosta* sub-zone is here proposed to take the place of Dr. Lang's *Liparoceras* sub-zone.

[2] See S. S. Buckman, 'Jurassic Chronology: I. Lias' Q. J. G. S. vol. lxxiii (1917–18) p. 264.

Middle Lias near Lincoln, and among them are bituberculate developments of *Oistoceras* (7, p. 104).

There are, therefore, not less than six widely-separated horizons with *striatus*-like forms, alternating with beds containing the different capricorn ammonites from which they have respectively evolved. Details of the correlation are given in Table I; the hemeral terms given for comparison are those recently proposed by Mr. S. S. Buckman, to whom I am indebted for the loan of his

TABLE I, *showing the chief areas where Liparoceratid horizons are developed.*

Hemeral Terms	Dorset	Cheltenham District	Warwickshire & N. Glos.	Lincoln	Yorkshire	Zones		Ranges of Genera
(MIDDLE LIAS with Liparoceratids)	×		×			margaritatus zone		Parinodiceras; Liparoceras; Becheiceras; Amisolobiceras; Androgynoceras; Oistoceras; Aegoceras; Amblycoceras
Oistoceras	×			×	×	davœi zone	Oistoceras sub-zone	
'henleyi'	×			×			dædalicosta sub-zone	
davœi	×			×				
brevilobatum		×			?		latæcosta sub-zone	
latæcosta	×	×	×	×	×			
Beaniceras	×	×	×	×	×	ibex zone		
carinatum	×	?						
cheltiense	×	×	×	?	×			
valdani	×	×	×	×				
ibex	×	×	×		?			

[The hemeral terms used are mainly those proposed by Mr. S. S. Buckman in Q. J. G. S. vol. lxxiii (1917–18) pp. 264–266.]

notes on the correlation of these beds. The corresponding sub-zones are also shown. It must be borne in mind that an understanding of the relationships of the ammonites is only possible when their horizons are accurately known; the details of the ammonite succession within the sub-zones must, therefore, be studied. The best time-scale is obviously supplied by a sequence of forms which are genetically connected, but a time-scale based on an evolutionary series (or a number of such series) cannot readily be constructed for the Liassic rocks of England, because, except within small limits, the ammonites of the Lias did not evolve here, our faunas probably representing successive immigrations. Consequently, an ideal correlation is not at present possible.

IV. General Evolution.

It is shown in the preceding notes that in the upper zones of the Lower Lias occur ammonites of several genera, which evolve from slender capricorns with stout ribs to involute bituberculate forms with swollen globose whorls, and that the morphic equivalents on separate lines of descent are so similar in certain cases as to present some difficulty in identification, unless sutural and other minute characters are taken into consideration. Further, the several series are not quite contemporaneous, morphic equivalents of different genera occurring at considerable intervals, and thus the precise geological age of one of these ammonites can only be determined when its lineage is known. It will be convenient now to consider the general trend of evolution in the characters which are common to all the series.

Early capricorns of this family show lateral ribbing at a diameter of 3 mm. or thereabouts, no ribs being present on the periphery until much later. In more advanced capricorns, however, the ribs appear, by tachygenesis, at about the diameter of 2 mm.

In the latter forms, at a diameter of about 100 mm., the ribs of the last whorl are frequently more widely-spaced, and may acquire small tubercles. In slightly later members of each series this condition is accompanied by a rapid expansion of the last whorl, the ribs becoming more slender and bearing paired tubercles; the ammonite is then of the *heterogenes*-type. The whorls are at first smooth and thick, become slender and only slightly embracing, later becoming stout again, the development of this latter condition thus being indirect. From this point onwards the tendency in evolution is to shorten the period of slender costate whorls and to hurry on to the bituberculate condition. This is accomplished by

(1) The acceleration of the development of the (secondary) swollen whorls, and of the bituberculation.

(2) The prolongation of the stage of smooth and globose whorls.

As a result, the stage of slender whorls with capricorn ornament is ultimately 'skipped' entirely in development. An example will make this clear. In specimen A, shown diagrammatically in Table II, capricorn ornamentation is developed at a diameter of 2 mm., and the shell does not become bituberculate until a diameter of 90 mm. Succeeding forms (B, C) retain the smooth globose whorls until diameters of 3 mm. and 5 mm. respectively, the bituberculation commencing earlier in each; thus the length of whorl with capricorn ornament in successive specimens of a lineage gradually becomes shorter, until ultimately bituberculation appears without any previous capricorn stage (D, E). In the last-mentioned forms the primitive smooth condition is retained much longer than in the immediate ancestors.

The occurrence of such a series of specimens on each of the lineages examined confirms the conclusion that the smooth inner

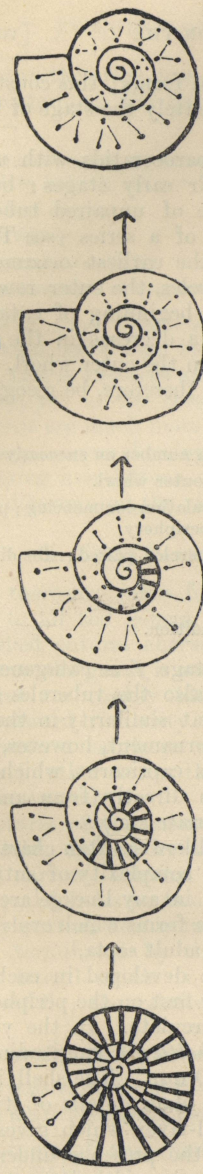


TABLE II.—*Diagram illustrating the ornament stages of a series of five ammonites (A–E) from a lineage of imparinode forms.*

[The 'skipping' of the capricorn stage is shown, but coiling stages are not shown.]

whorls of the more advanced members are not an indication of different origin from the ammonites which pass through a capricorn stage; this skipping of the capricorn stage during development (saltative palingenesis)[1] being

> 'a compromise due to the necessity of attaining as perfect a condition as possible in as short a time as possible, for the sooner the adult condition is reached the sooner will the organism be able to reproduce its kind.'[2]

Owing to the method of origin of the tubercles as points on the ribs, they are at first necessarily arranged in pairs. When the whorl becomes swollen, however, the line of outer tubercles is much longer than the line of inner tubercles; in many series the number of outer tubercles progressively increases, until it may be double the number of the inner tubercles.

From this stage, therefore, two distinct groups of Liparoceratid ammonites may be recognized, namely:—

(1) An earlier group with tubercles paired in the globose stages (parinode forms).

(2) A later group with tubercles unpaired in the globose stages (imparinode forms).

Almost all British Liparoceratids belong to the second group[3]; Quenstedt's figures show, however (4, pl. xxviii, figs. 16–23), that ammonites of the first group (*A. striatus parinodus*) are of fairly common occurrence on the Continent. In considering the second group it is often convenient to express the ratio of outer to inner tubercles as a fraction, the ratio

[1] Since this paper was read Dr. W. D. Lang has suggested the term 'lipogenesis' in place of saltative palingenesis (Proc. Geol. Assoc. vol. xxx, 1919, p. 60).

[2] A. Dendy, 'Outlines of Evolutionary Biology' 2nd ed. (1912) p. 273.

[3] I have examined only nine British Liparoceratids in the sphærocone stage with paired tubercles; these were collected at a low horizon at Radstock, Somerset (see p. 264).

generally increasing with more advanced forms; this constitutes a ready method of determining approximately the stage of advance of any specimen.

It must be recognized that most Liparoceratids with unpaired tubercles have paired tubercles in their early stages; but, with acceleration of development, the stage of unpaired tubercles is reached earlier in successive members of a series (see Table II, D, E), and in very advanced forms the earliest ornamentation acquired may consist of unpaired tubercles, the outer row having double the number of the inner. The beginning of catagenesis, on the other hand, may be shown by a decrease in the ratio of the number of outer to inner tubercles on the outer whorl.

The following ornament stages may, therefore, be recognized in most lineages:—

(*a*) Capricorn ribs, regularly increasing in number on successive whorls.

(*b*) Capricorn ribs, widely spaced on the outer whorl.

(*c*) Capricorn ribs widely spaced, bituberculation commencing; prominent striations between the ribs on the periphery.

(*d*) Ribs more slender, bituberculate, tubercles paired; ribs dividing on the periphery.

(*e*) Similar, but with tubercles unpaired.

(*f*) Tubercles returning to the paired condition.

The stages *a* to *e* are anagenetic; stage *f* is catagenetic. In the later stages of many sphærocones also the tubercles are finer than in the early stage, leading to great similarity in the several series (homœomorphy). Catagenetic ornament, however, is occasionally seen in the old age of various capricorns, which do not attain the tuberculate stage, but pass directly from anagenetic costate to catagenetic subcostate and striate stages.

Successive members of the series are likewise often characterized by increasing involution and by greater complexity of suture-line. Thus the simple sutures of a capricorn in any lineage are closely comparable with the early sutures of the forms which evolved from it, and with the septal sections of their adult septa.[1]

Longitudinal striations appear to be developed in each of the series considered here, usually appearing first on the periphery soon after the whorls are swollen and bituberculate. In the young of advanced species, such as *Liparoceras cheltiense*, longitudinal striations are developed at a diameter of 20 mm. The shell is rarely well-preserved, and thin sections do not show details of structure: the slight corrugation of the outer shell-layer which gives rise to the striate appearance is often due to the presence underneath it of sharply-defined parallel ridges varying in width, but rarely more than ·5 mm. across, and not more than 1 mm. apart (see 4, pl. xxix, fig. 7 *x*). It is possible, however, that in some cases the underlying ridges are not present, or are lost in subsequent development.

[1] H. H. Swinnerton & A. E. Trueman, 'The Morphology & Development of the Ammonite Septum' Q. J. G. S. vol. lxxiii (1917–18) p. 26.

There are, therefore, five progressive characters which may be used to determine the position of any specimen in its series, namely:—

(1) Ornamentation, progressing from smooth, and costate, to bituberculate (paired) and possibly bituberculate (unpaired).
(2) Whorl shape.
(3) Involution.
(4) Sutural complexity.
(5) Development of longitudinal striations.

Certain of these characters are acquired at a relatively earlier stage in some series than in others; thus the sutures of the capricorns of *Androgynoceras* and *Liparoceras* are similar in degree of complexity, yet in the corresponding later forms the sutures of *Liparoceras* are much more complicated than those of specimens of *Androgynoceras* showing similar involution and tubercle-ratio. The differing associations of these characters will, therefore, be useful in determining the various lineages.

V. Systematic Study of the Genera.

While there are many features in the adult sutures which are common to all the genera, there are nevertheless some readily-distinguished sutural characters which make their identification easy. Once the genus is accurately determined the species within each genus are readily identified, for there is naturally much greater outward similarity between the capricorns of two series than between a capricorn and its later development in the same series—or, in other words, the chief difficulty lies in the distinction of morphic equivalents.

The sutures of the ammonites studied agree in having a deep external lobe, divided by a median saddle which is usually very high and narrow; external saddles high, often divided into three very unequal folioles by two denticulations, that of the dorsal side frequently cutting deeply into the saddle. The first lateral lobe is generally terminated by three lobules, sometimes asymmetrical. The first lateral saddle is narrow, and always smaller than the external saddle; the relatively simple auxiliaries are of variable number.

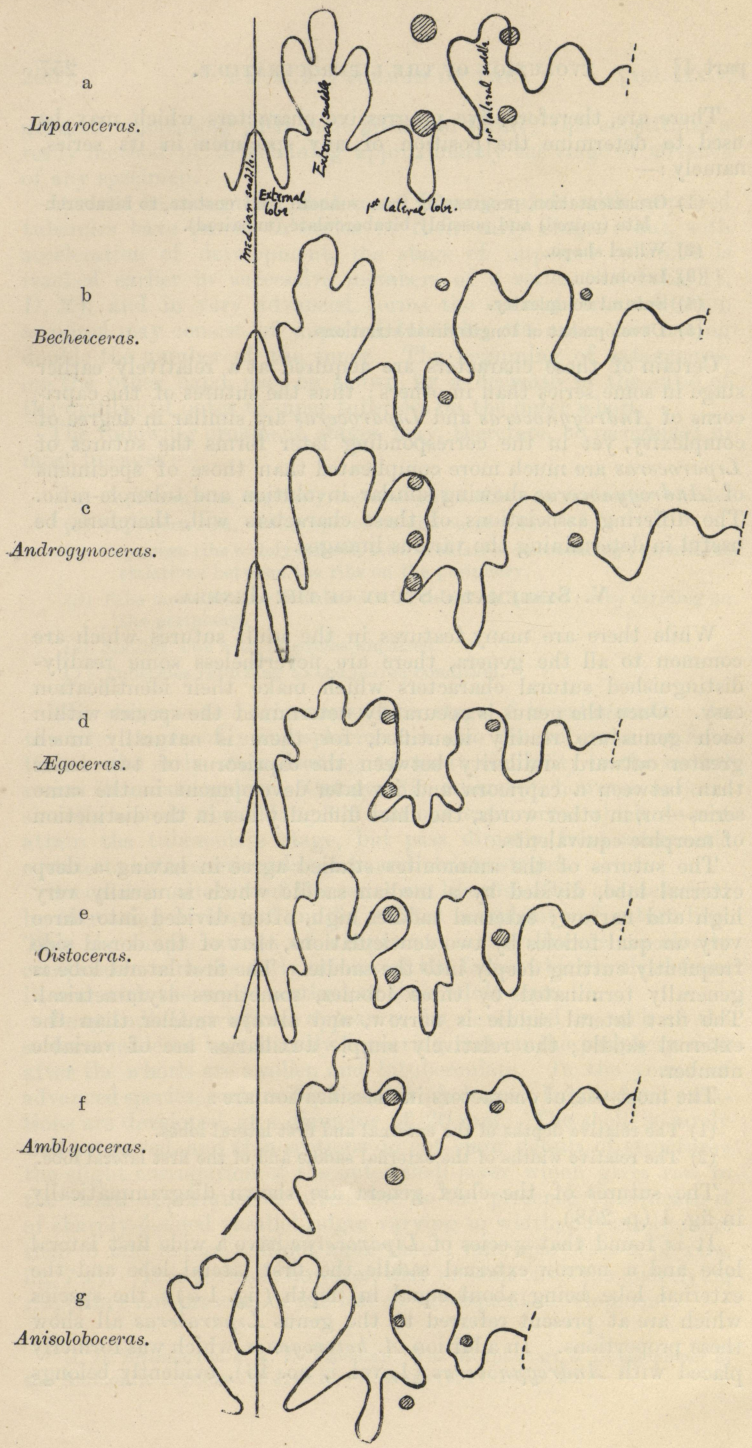
The most useful characters in classification are:

(1) The relative depths of the external and first lateral lobes.
(2) The relative widths of the external saddle and of the first lateral lobe.

The sutures of the chief genera are shown diagrammatically in fig. 1 (p. 258).

It is found that species of *Liparoceras* have a wide first lateral lobe and a narrow external saddle, the first lateral lobe and the external lobe being about equal in depth (fig. 1 *a*); the species which are at present referred to the genus *Liparoceras* all show these proportions. In addition *A. heterogenes*, which was formerly placed with *Androgynoceras* (1, vol. i, no. 46), evidently belongs

Fig. 1.—*Outline sutures of the principal Liparoceratid genera.*



to the genus *Liparoceras*; *A. bechei* and *A. henleyi*, which were formerly placed together as species of *Androgynoceras*, have very different sutures, that of the latter resembling the genotype of *Ægoceras* (fig. 1 *d*), while it is necessary to establish a new genus to include the *A. bechei* series (fig. 1 *b*). The sutures of *Amblycoceras* are likewise very characteristic, having a first lateral lobe much shallower than the external lobe (fig. 1 *f*).

A. nautiliformis, which Mr. Buckman inferred from stratigraphical and other evidence was the sphærocone of the *Ægoceras* series, has a suture [1] which differs markedly from that of all other British Liparoceratids, and resembles those of similar sphærocones in the Swabian Jura (4, pl. xxix, figs. 4–6) and of certain capricorns (as, for example, *A. adnethicus* and *A. ferstli*) also found on the Continent.[2] The suture of these ammonites has an external lobe much smaller than the first lateral lobe, the ventral lobules of which almost meet underneath the external lobe, a condition that recalls certain Deroceratids (fig. 1 *g*).

It is extremely probable that in the Lias of the Continent occur not only many species which are not represented in this country, but also several genera. It is not safe to assume, therefore, that the capricorns referred to *A. adnethicus* are the ancestors of *A. nautiliformis*; the range of this series (from the ? *valdani* zone to the *margaritatus* zone) would be unusually great. For this reason *A. adnethicus* and *A. ferstli* are only referred provisionally to the genus *Anisoloboceras*, which is proposed to include ammonites of the *A. nautiliformis* type. The Continental ammonites of the Liparoceratidæ should be fully studied before any attempt to classify them is made, since any arrangement based only on a consideration of the published figures would necessarily be provisional and would ultimately lead to greater confusion.[3]

(1) Series in which the Sphærocones have Unpaired Tubercles.

Liparoceras Hyatt, 1867.

Genolectotype: *Ammonites striatus* Bronn.

Genus passing from costate serpenticone (capricorn) to bituberculate sphærocone. Whorl usually depressed, venter nearly flat or with a low arch; ornament generally coarse, the ribs passing with little or no curve across the periphery.

Body-chamber nearly one whorl.

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[1] I am indebted to Mr. Buckman for kindly supplying a sketch of the suture of the type-specimen, which was formerly in his possession and now is in the Manchester Museum.

[2] See F. von Hauer, 'Beiträge zur Kenntniss der Capricornier der Œsterreichischen Alpen' Sitzungsb. K. Akad. Wissensch. Wien, vol. xiii (1854) pp. 94–121, and P. Reynès, 'Monographie des Ammonites' 1879, pl. xxx, figs. 9 & 10.

[3] It may be mentioned here that many of the published figures of Continental forms are not mentioned in this paper, as they frequently do not show sufficient detail to allow of even approximate correlation, while in other cases the specimens are evidently quite different from anything that has been found in Britain.

Suture: EL and IL about equal in depth, wider than ES, IL generally trifid (fig. 1 *a*).

Species included:—

L. sparsicosta, sp. nov., *L. heterogenes* (Young & Bird), *L. obtusinodum*, sp. nov., *L. zieteni* (Quenstedt), *L. heptangulare* (Young & Bird), *L. cheltiense* (Murchison).

L. tiara, sp. nov.

L. pseudostriatum, sp. nov.

Geological horizon: Upper part of the *ibex* zone.

The ammonites comprising the genus *Liparoceras* range from stout capricorns to moderately involute thick-whorled forms with generally coarse bituberculation. The best-known English ammonite belonging to this series has been called *Liparoceras striatum*; Reinecke's figure of this species, however, shows an involute depressed Liparoceratid with paired tubercles on the outer whorl (5, pl. viii, figs. 65 & 66). Involute Liparoceratan forms from the British Lias have the tubercles unpaired, the outer being nearly twice as numerous as the inner. It is probable, therefore, that *L. striatum* (Reinecke) does not occur in this country, and it may be a representative of another lineage, probably allied to *A. striatus parinodus* Quenstedt (4, pl. xxix); *L. pseudostriatum* is here proposed for some of the English ammonites which have been called *L. striatum*. The similar fossils from Gloucestershire are members of the same genus, and include a number of forms closely allied to *L. cheltiense*.

The capricorns from which these ammonites arose have not hitherto been noticed, but are here described as *L. sparsicosta* (Pl. XXI, fig. 2), while *L. heterogenes* is a later stage (biologically, at least) in the same series, having fine paired tubercles on the outer whorl.

A number of intermediate forms unite this with ammonites resembling *L. obtusinodum*, which has fine paired tubercles on the inner whorls, but develops coarse unpaired tubercles on the outer whorl. A further stage is shown by *L. cheltiense*, in which the earliest tubercles are fine and unpaired, later becoming stronger, and finally transversely elongated on the last whorl, the commencement of catagenesis being indicated by a tendency to return to paired tubercles. More advanced ammonites of this lineage have finer tubercles on the outer whorl. *Liparoceras heptangulare* is probably a related species, which may be connected with *L. zieteni*, since both these species have a peripheral arch more pronounced than is usual in the genus.

Several other series of Liparoceratan ammonites may be distinguished, although the material available for their study is insufficient for the establishment of lineages—one such series comprises ammonites that develop fine ornamentation only (*L. pseudostriatum*). The above forms usually become comparatively involute, but at least one series retained a moderately evolute form with coarse unpaired tubercles. This series includes *L. tiara* (Pl. XXI, fig. 1), which, notwithstanding its wide umbilicus, has a very complicated suture with deeply undercut saddles (fig. 4 *d*, p. 270), suggesting that it is at least as advanced as *L. cheltiense*.

ANDROGYNOCERAS Hyatt, 1867.

Genolectotype: *Ammonites hybrida* A. d'Orbigny (3, pl xxxv, figs. 1–3, *non* 4–5).

Develops from capricorn to bituberculate sphærocone. Whorl height usually about equal to whorl thickness. Ornamentation never so coarse as in some species of *Liparoceras*, and not usually so fine as in *Becheiceras*.

Suture: EL and IL about equal in depth, IL with lobules usually asymmetrical, very narrow, and ES very wide (fig. 1 *c*, p. 258). Body-chamber about three-quarters of a whorl.

Species included[1]:—

A. maculatum (Young & Bird), *A. obtusicosta*, sp. nov., *A. hybrida* (d'Orbigny), *A. divaricosta*, sp. nov.

Horizon: *Davœi* zone, extending from the *latæcosta* sub-zone to the *dædalicosta* sub-zone.

In the development of *Androgynoceras* the outer tubercles appear first; *A. henleyi* Reynès, in which the inner tubercles are much more prominent than the outer, probably belongs to a different series. Involution proceeds slowly, and no specimen has yet been examined in which the outer tubercles are twice as numerous as the inner.

The more involute forms of this lineage have hitherto been found only at Lincoln (7, p. 104).

ÆGOCERAS Waagen, 1869.

Genolectotype: *Ammonites planicosta* A. d'Orbigny.

Develops from capricorn to bituberculate sphærocone. Whorl height usually about equal to whorl thickness. Ornamentation moderately fine, usually a little coarser than that of *Androgynoceras*.

Suture: EL and IL about equal in depth; IL usually small, and terminated by three fairly-symmetrical lobules; the median lobule frequently short; ES very wide (fig. 1 *d*, p. 258). Body-chamber nearly a whorl in length.

Species included:—

A. æquicosta, sp. nov., *A. latæcosta* (Sowerby), ?*A. henleyi* (Sowerby), *A. dædalicosta*, sp. nov.

Horizon: *Davœi* zone, extending from the *latæcosta* sub-zone to the *dædalicosta* sub-zone.

The ammonites of this series are not very different from those of the *Androgynoceras* series; generally the first lateral lobe in *Ægoceras* is smaller and more symmetrical than in *Androgynoceras*. The sphærocones are also distinct, but the separation of these series is not easy.

The young, before ribs are developed on the periphery, are scarcely distinguished from similar stages in the *Amblycoceras* and *Oistoceras* series. Thus ribs appear at approximately the same diameter, and sutural development at first proceeds similarly in each group. It seems, therefore, probable that these four genera had a common origin, and are much more closely related than any other Liparoceratid genera dealt with in this paper. (See Table III, p. 286.)

[1] Several earlier species (*A. integricostatum*, *A. siphunculare*) are also referred to this genus (see p. 290), but it is probable that the genera *Ægoceras* and *Androgynoceras* had not at that time become separated.

AMBLYCOCERAS Hyatt, 1900.

Genoholotype: *A. capricornus* Hyatt.[1]
Develops from capricorn to a form with bituberculate swollen outer whorl. The costæ are very little diminished on the periphery of the capricorns, and shw a distinct forward bend, less sharp than that of *Oistoceras*.
Suture: IL much shallower than EL, which usually has a short and wide median saddle. IL has three subequal terminal lobules. ES wide, with three terminal cells (fig. 1*f*, p. 258).
Species included:—
A. crescens Hyatt, *A. dissotypum*, sp. nov., *A. brevilobatum*, sp. nov.
Horizon: *Davœi* zone (*latæcosta* sub-zone to *Oistoceras* sub-zone).

The ammonites of this genus are of two series: the earlier, which includes *A. brevilobatum*, has slender elevated whorls with close and uniform costæ; and the later, including *A. crescens*, has stout whorls, with prominent costæ separated by wide concave spaces on the outer whorl. Bituberculate forms are known in both series. The *A. crescens* series is not derived from the earlier, for *A. crescens* retains the primitive depressed whorl; its inner whorls, however, have numerous ribs and are similar in form to the young of *A. brevilobatum*. It is probable that this latter group represents an offshoot from a primitive *crescens*-like stock.

OISTOCERAS S. S. Buckman, 1910.

Genoholotype: *O. figulinum* (Simpson). (Refigured, 1, vol. i, No. 26.)
Develops from a capricorn to a bituberculate form with swollen whorls; the costæ are little diminished on the periphery, where they have a very marked forward curve, much greater than in *Amblycoceras* ('arrow-like peripheral costæ').[2]
Suture: EL and IL about equal in depth, EL narrow and with a high median saddle in the later forms; IL frequently asymmetrical (fig. 1 *e*, p. 258).
Species included:—
O. figulinum (Simpson), *O. allœotypum*, sp. nov., *O. omissum* (Simpson), *O. curvicornum* (Schlœnbach).
Horizon: ? *dædalicosta* sub-zone to lower part of *margaritatus* zone (at Lincoln only). Dominant in the *Oistoceras* sub-zone.

Two series may be recognized among the ammonites of this genus, namely:—

(1) With squared venter, developing coarse bituberculation (*O. curvicornum* Wright, *non* Schlœnbach).

(2) With a rounded or subangular venter, developing fine bituberculation (*O. allœotypum*, Pl. XXV, fig. 1). Some forms of the latter series have a peripheral rib-curve not much stronger than that of *Amblycoceras*; they may be distinguished from the latter genus, however, by sutural characters. Similarly, occasional specimens of *Amblycoceras* have a rib-curve equal to that of *Oistoceras* (see p. 279).

[1] In Eastman-Zittel, 'Text-book of Palæontology' 1st ed. vol. i (1900) fig. 1204, p. 578.
[2] See 1, vol. i, p. *iv*.

Although the genera *Androgynoceras*, *Ægoceras*, *Amblycoceras*, and *Oistoceras* have typically ribs almost straight, slightly curved, and markedly curved on the periphery, *Amblycoceras* must not be considered as intermediate between *Oistoceras* and *Androgynoceras* or *Ægoceras*, for the sutures of *Oistoceras* are frequently very similar to the sutures of *Androgynoceras* (compare, for example, the first lateral lobes in fig. 8 *c*, p. 278 & fig. 12 *a*, p. 285), while the sutures of *Amblycoceras* often resemble those of *Ægoceras*, except that the first lateral lobe is shallower in *Amblycoceras*. It may, therefore, be suggested that *Oistoceras* and *Amblycoceras* arose from primitive members of the *Androgynoceras* and *Ægoceras* stocks respectively: probably before the latter had acquired peripheral costæ, but after the sutural characters of the two last-named genera had become distinct.

BECHEICERAS, gen. nov.

Genoholotype: *A. bechei* Wright (8, pl. xli, figs. 1 & 2).

In this series sphærocones only are known [1]; these are finely ornamented, bituberculate (unpaired). In development of the sphærocones the capricorn stage is omitted. Longitudinal striations are well developed.

Suture: EL not so deep as IL, which is often wider than ES, thus the greater part of IL is frequently ventral to the outer tubercles (fig. 1 *b*, p. 258).

Horizon.—*Dædalicosta* and *Oistoceras* sub-zones.

The suture is most like that of *Liparoceras*, differing mainly in the deeper first lateral lobe: *Becheiceras* is, therefore, very similar to the finely-ornamented involute *Liparoceras*, but its horizon is much higher.

ANISOLOBOCERAS, gen. nov.

Genoholotype: *A. nautiliformis* J. Buckman (1, vol. i, No. 37).

Includes capricorn forms and very stout bituberculate sphærocones with fine ornament.

Suture: EL much shallower than IL, the ventral lobules of the IL almost uniting under the EL (fig. 1 *g*, p. 258).

Species included:—

? *A. adnethicus* Hauer, ? *A. ferstli* Hauer, *A. spinellii* Hauer, *A. nautiliformis* J. Buckman.

Horizon.—The sphærocones, which alone occur in Britain, are found in the *margaritatus* zone; the horizon of the capricorn forms which are provisionally referred to this genus is probably near the *ibex* zone.

A. nautiliformis was placed with *Ægoceras* by Mr. Buckman, who had not compared the sutures of these ammonites. The difference in sutural proportions has already been pointed out (p. 259).

The capricorns from the Adneth Shales described by F. von Hauer,[2] are provisionally referred to this genus, but their precise

[1] *Ægoceras capricornu* var. *nodosa* Futterer, 'Die Ammoniten des Mittleren Lias von Œstringen' Mitt. Bad. Geol. Landesanst. vol. ii (1893) pl. xi, figs. 1 & 2, may be near the capricorns of this series.

[2] 'Beiträge zur Kenntniss der Capricornier der Œsterreichischen Alpen' Sitzungsb. K. Akad. Wissensch. Wien, vol. xiii (1854) p. 101.

horizon is unknown, and apparently no comparable forms have been discovered in this country. *A. spinellii*, also described by F. von Hauer,[1] is the small young of the sphærocone in which the capricorn stage is omitted[2]; the sutural proportions are suggestive of this genus.

Of *A. nautiliformis*, Mr. Buckman figured two specimens, of which the former (the holotype) is somewhat stouter (1, vol. i, No. 37). Some ammonites figured by Quenstedt (4, pl. xxix) agree in whorl shape, suture, and position of tubercles; the horizon given by Quenstedt is similarly considerably higher than the horizon of other sphærocones.

(2) Series in which the Sphærocones have Paired Tubercles.

It is not possible to offer any detailed classification of these forms, which do not occur commonly in this country and of which very little material is available. It appears, however, that three series may be recognized, namely:—

(1) A parinode series with depressed whorl; this includes *A. striatus* Reinecke. No representative of the group has been recorded in this country.

(2) A parinode series with elevated whorl; this includes *A. striatus parinodus* Quenstedt (4, pl. xxviii, figs. 16–23), *A. striatus lævis* Quenstedt (4, pl. xxviii, fig. 6), *A. striatus reineckii* Quenstedt (4, pl. xxviii, fig. 5). Sphærocones of this series, in the collections of Mr. S. S. Buckman and Mr. J. W. Tutcher, from the *valdani* zone of Radstock, resemble the last-named species.

To cover this series the genus *Parinodiceras* is here proposed. Genoholotype, *Ammonites striatus parinodus* Quenstedt (4, pl. xxviii, fig. 16).

(3) A parinode series with round whorls; the tubercles of the inner row are placed high up the whorl, so that the two rows are unusually close together. Only three examples are known, in the collection of Mr. J. W. Tutcher, who obtained them from the *valdani* zone of Radstock.

The name *Vicininodiceras* is proposed for this series. Genoholotype, *V. simplicicosta*, sp. nov. (Pl. XXIV, fig. 4.)

It will be noted that all the parinode forms which have been observed in England occur at a lower horizon than any imparinode forms, and probably represent a more primitive stage in evolution.

Notes on Phricodoceras Hyatt, 1900.

Genoholotype: *Phricodoceras (Ammonites) taylori* (A. d'Orbigny). (3, pl. cii, figs. 3 & 4.)

This genus of Liparoceratid ammonites is not fully considered

[1] 'Ueber die Ammoniten aus dem sogenannten Medolo der Berge Domaro' Sitzungsb. K. Akad. Wissensch. Wien, vol. xliv (1861).

[2] *Ammonites henleyi* Hauer, 'Ueber die Cephalopoden aus dem Lias der Nordöstlichen Alpen' Denkschr. K. Akad. Wissensch. Wien, vol. xi (1856) p. 60 & pl. xx, figs. 4–6, may be a coarsely-tuberculate form of this genus.

here, since its evolution is different from that of the series described above. *Phricodoceras* includes the *taylori* group of ammonites: these forms rapidly acquire bituberculation or even trituberculation, without any marked expansion of the whorl such as is characteristic of the genera hitherto dealt with.

Mr. Buckman has called my attention to a specimen of *Phricodoceras lamellosum* (A. d'Orbigny) from the *armatus* zone of Radstock, in his collection (No. 2917), in which the strongly tuberculate stage is followed by a stage with feeble ornament and a great increase in the size of the whorl, the outer whorls thus bearing some resemblances to the involute forms of the preceding genera. It is distinguished by

(1) The greater elevation of the outer whorl,
(2) Enlargement of the whorl subsequent to the acme of ornamentation,
(3) The close approximation of the outer tubercles to the ventral margin.

Ammonites striatus bicornis Quenstedt (4, pl. xxviii, fig. 24) and *A. taylori* Quenstedt (4, pl. xxvii, fig. 19) show a similarly expanded outer whorl with catagenetic ornament.

VI. Study of Species and Developmental Details.

A. Liparoceras.

Liparoceras sparsicosta, sp. nov. (Pl. XXI, figs. 2 *a*–2 *b* & 3 *a*–3 *e*; text-figs. 2 *a*–2 *g*, p. 266.)

Dimensions of holotype :—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
35 mm.	32 per cent.	35 per cent.	44 per cent.

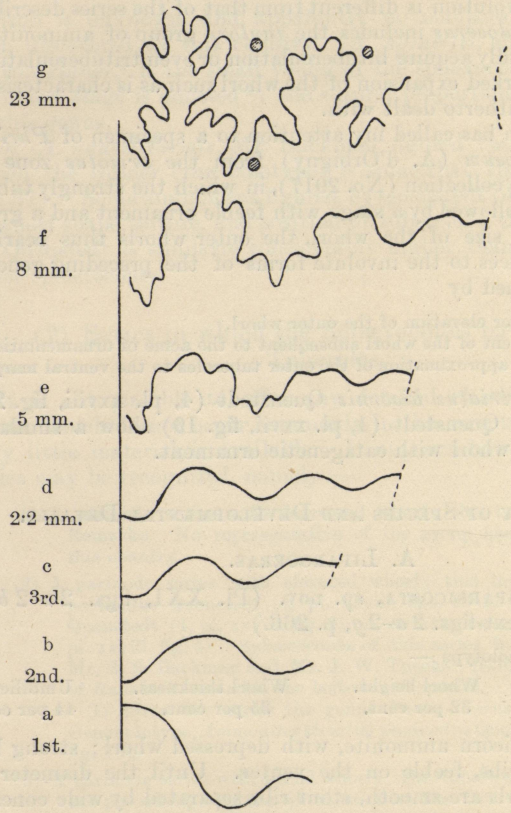
A small capricorn ammonite, with depressed whorl; strong but widely-spaced ribs, feeble on the venter. Until the diameter of 6 mm. the whorls are smooth, stout ribs separated by wide concave spaces appearing at that diameter. Thirteen ribs on the outer whorl, of which the last nine have paired tubercles; periphery broad, with the low arch characteristic of the genus.

At 22 mm. diameter the suture is moderately simple, but shows the feature of the genus, namely: the first lateral lobe is wider than the external saddle, and about equal in depth to the external lobe, thus part of the first lateral lobe is ventral to the outer line of tubercles (text-fig. 2 *g*, p. 266).

The type-specimen was collected by Mr. L. Richardson, F.G.S., from a well at Queen's Wood Cottages, Prestbury, near Cheltenham. Specimens may also be obtained at a similar horizon at Napton (Warwickshire), and at Dumbleton (Gloucestershire).

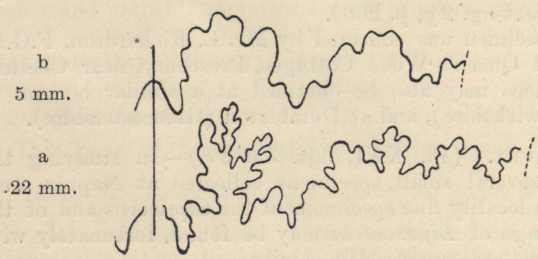
Development. (Pl. XXI, figs. 3 *a*–3 *e*.)—In studying the development several small specimens collected at Napton were used. In this locality fine specimens of the capricorns and of the *heterogenes* stage of *Liparoceras* may be found, fortunately with the inner whorls well preserved in calcite.

Fig. 2.—*Sutural development of* Liparoceras sparsicosta.



[g=L. Richardson Coll., figured in Pl. XXI, fig. 2 *a*.]

Fig. 3.—*Sutures of* Beaniceras *spp. (Napton)*.



The protoconch shows the usual characters (Pl. XXI, fig. 3 *d*), its length being 0·68 mm. Shell development proceeds normally for some time; thus there is a general increase in the size of the whorl, whorl height at first increasing proportionately more rapidly than whorl thickness. The shell remains smooth until a diameter of 5 mm. is reached, when there appear on the sides widely-separated ribs, which do not cross the venter until later (diameter 10 mm.). The whorl thickness increases regularly, but the whorl remains depressed much longer than is usual in capricorns (see Pl. XXI, fig. 3 *a*) which generally acquire slender, nearly round whorls at a diameter of 3 mm. Thus, it will be seen from the following table that, in *Liparoceras sparsicosta*, the whorl height is less than the whorl thickness, even at a diameter of 20 mm. This retention of the early depressed shape and smooth whorls may point to the primitive nature of *L. sparsicosta*; it is probable, however, that these features indicate that this ammonite is already beyond the true capricorn stage, and that the depressed inner whorls are due to the prolongation of the primitive globose form.

Diameter. mm.	Whorl height. per cent.	Whorl thickness. per cent.	Umbilicus. per cent.
·58	48	119	—
·68	42	96	28
1·14	42	69	30
1·8	40	65	—
3·6	39	55	29
8·0	28	55	—
16·0	28	46	36
20·0	33	45	35

The first suture shows typical angustisellate characters (text-fig. 2 *a*). At the second suture the azygous saddle is divided by a fairly deep ventral lobe, which is deeper than the corresponding lobe in the second suture of other capricorns (text-fig. 2 *b*). In the third suture the ventral lobe has a small median saddle; there is little advance on this stage during the next whorl, the median ventral saddle becoming slightly more pronounced and an auxiliary saddle appearing at the umbilical margin (text-fig. 2 *d*). A very feeble denticulation appears on the dorsal margin of the external saddle at a diameter of 4·5 mm., and a little later the saddle has three terminal cells and the first lateral lobe three lobules. Subsequent development leads to the increase in height of the external saddle and in depth and width of the first lateral lobe; these attain adult proportions at a diameter of 10 mm., all the elements later becoming complicated by minor denticulations.

Distinctions.—*Androgynoceras maculatum* is the only capricorn among the British Liparoceratidæ from which *Liparoceras sparsicosta* is not readily distinguished; *A. maculatum* has similarly widely-spaced ribs (about seventeen to a whorl; some capricorns may have thirty) which are feeble on the venter. In *A. maculatum*, however, whorl height is greater than whorl thickness,

while the venter is well rounded and does not show the low arch of *Liparoceras*.

It is more difficult to separate *L. sparsicosta* from certain species of *Beaniceras*. Mr. Buckman proposed this latter genus to include *A. luridum* (1, vol. ii, p. *iii*) placing it with the Liparoceratidæ, but its affinities are with the Dactyloids rather than with the Liparoceratids (see p. 292). *Beaniceras luridum* is a capricorn form, probably a catagenetic descendant of a tuberculate cadicone (that is, a form with the whorl thickest at the ventral margin); such cadicones of the *Beaniceras* series have been detected at Napton and elsewhere, and with them also occur ammonites which resemble *B. luridum*, and have strongly-ornamented cadicone inner whorls, the outer whorl having normal capricorn ornament, in some cases very similar to that of *L. sparsicosta*. The young of such a form is figured in Pl. XXIII, fig. 2, the shape of the whorl being very different from that of the young of *Liparoceras sparsicosta* (Pl. XXI, fig. 3 *a*). The chief points of distinction of these series are:

(1) The stronger ornament of the inner whorls of *Beaniceras*; the capricorns of the *Beaniceras* series are catagenetic, those of the Liparoceratidæ are anagenetic.

(2) The steep central part of the umbilicus of *Beaniceras* (due to the cadicone inner whorls).

(3) The suture of *Beaniceras* frequently shows a ∧-shaped median cell, as was pointed out by Mr. S. S. Buckman (1, vol. ii, No. 73).

This last-named character, however, is not constant; it is not always present in *Beaniceras*, and may sometimes be seen in other capricorns. The arrangement of the sutural elements is somewhat similar in *Liparoceras* and *Beaniceras*; in Napton specimens of the latter the first lateral lobe is relatively wider. In development, the sutures of *Beaniceras* are more complicated than the sutures of *Liparoceras* at similar diameters. Thus the suture of *Beaniceras* at 5 mm. (text-fig. 3 *b*, p. 266) is quite as advanced as that of *L. sparsicosta* at 15 mm.

LIPAROCERAS HETEROGENES (Young & Bird). (Fig. 4*e*, p. 270.)[1]

Refigured, *Androgynoceras heterogenes* (Young & Bird), S. S. Buckman (1, vol. i, No. 46).

Retains capricorn form up to a diameter of 60 mm., the last whorl being swollen; bituberculation commences earlier than in *L. sparsicosta*, certainly before a diameter of 20 mm. If *L. heterogenes* is properly assigned to the *Liparoceras* series it is probably a little more advanced than *L. sparsicosta*.

This species was formerly referred to the genus *Androgynoceras*, but it appears to belong to *Liparoceras*, since it shows whorl height

[1] The sutures shown in figs. 4 (*a*, *e*, *f*), 7, 8 (*a*, *b*), 10 (*b*, *c*), and 13 were drawn from the left-hand side of the specimens, but are here reversed for convenience in comparing them with others.

less than whorl thickness, and a broad low-arched venter, with the outer row of tubercles near the edge of the whorl. Although in the type-specimen no sutures are visible, yet specimens from Napton and Yorkshire which appear to be identical show sutures of the *Liparoceras* pattern (fig. 4 *e*) intermediate in degree of complexity between *L. sparsicosta* and *L. obtusinodum*.

A complete series of specimens may be arranged, transitional between *L. heterogenes* and *L. obtusinodum*. In successive members at a given diameter the whorl is stouter, the ratio of the numbers of outer to inner tubercles is greater, and the sutures are more complex. Further, the stage at which capricorn ornamentation is developed steadily becomes later, while bituberculation appears earlier, so that ultimately the capricorn stage is omitted, as shown in the table :—

	Diameter. mm.	Whorl height. per cent.	Whorl thickness. per cent.	Umbilicus. per cent.	Capricorn from diameter	to diameter.	Tubercle on last whorl.
From Napton, Warwick.	50	27	33	33	5	50	Paired.
	35	29	34	29	6	19	Paired.
	50	44	52	30	8	12	23/15
From Battledown, Cheltenham.	60	47	57	23	—	—	25/15
	60	48	56	20	—	—	23/12
	70	51	61	17	—	—	24/12

LIPAROCERAS OBTUSINODUM, sp. nov. (Fig. 4 *c*, p. 270.)

Dimensions of holotype (from Napton, Warwickshire) :—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
45 mm.	44 per cent.	52 per cent.	33 per cent.

Compare *Ammonites striatus* Bronn.[1]

Whorl depressed, venter nearly flat, umbilicus fairly small, the tubercles unpaired, about 22/18.

The inner whorls of *L. obtusinodum* have no capricorn stage, but the tubercles are fine and paired until the diameter of 25 mm.

L. obtusinodum occurs in Dorset in the Belemnite Stone and the beds immediately below it.[2] One such form (W. D. L. Coll. 1493) has the following dimensions :—

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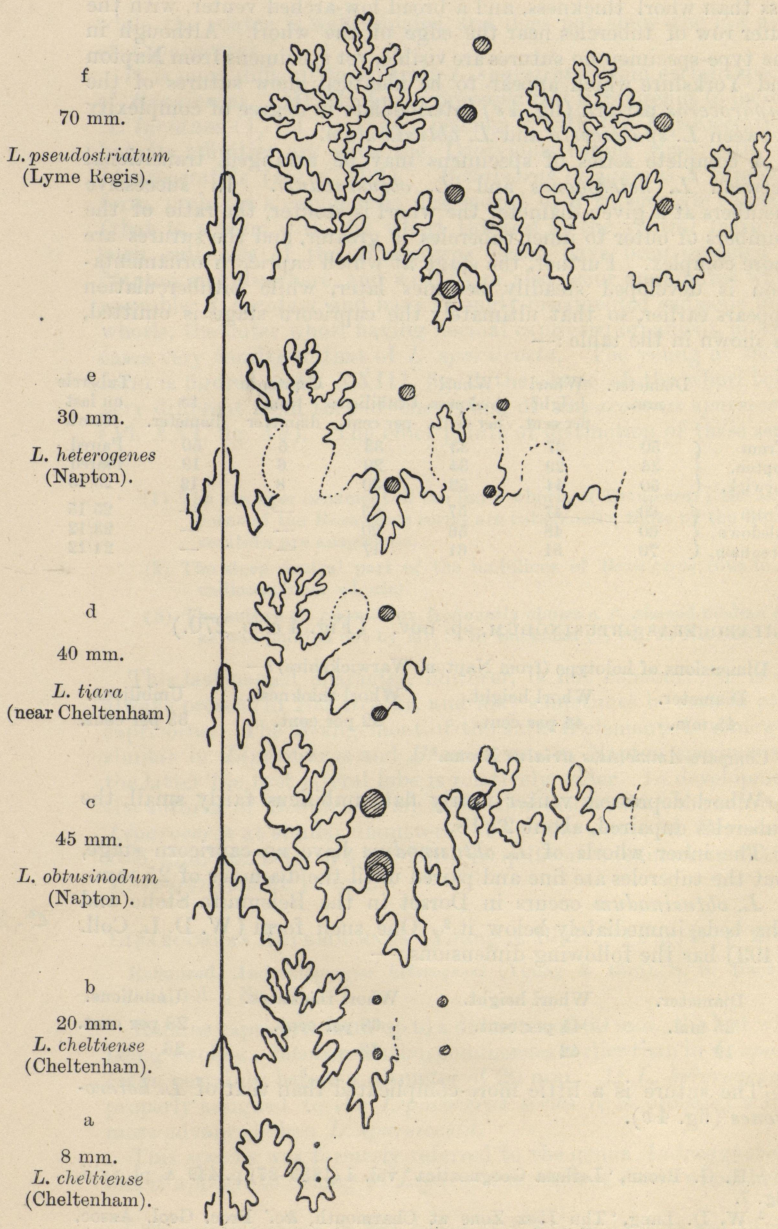
Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
25 mm.	44 per cent.	68 per cent.	28 per cent.
19	42	63	26

The suture is a little more complicated than that of *L. heterogenes* (fig. 4 *c*).

[1] H. G. Bronn, 'Lethæa Geognostica' vol. i (1835–37) p. 449 & pl. xxiii, fig. 7.

[2] W. D. Lang, 'The *Ibex* Zone at Charmouth, &c.' Proc. Geol. Assoc. vol. xxviii (1917) p. 33.

Fig. 4.—*Sutures of* Liparoceras *spp.*



LIPAROCERAS CHELTIENSE (Murchison). (Pl. XXI, figs. 4 *a*–4 *d*; text-figs. 4 *a* & 4 *b*, p. 270.)

Refigured, 'Palæontologia Universalis' pt. iii, ser. 1 (1905) No. 67.

Dimensions of figure :—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
93 mm.	45 per cent.	67 per cent.	24 per cent.

In the type-specimen the early part of the last whorl is similar in shape and ornament to *L. obtusinodum*. Towards the end of the whorl, however, the whorl height increases and the periphery becomes more strongly arched, while the unpaired rounded tubercles give place to paired bullæ or transversely extended tubercles : this return to paired tubercles is the first indication of catagenesis.

The details of the suture in the type-specimen are not discernible; but it is clear that the external saddle is narrower than the first lateral lobe, the latter being mainly ventral to the outer tubercles. (British Museum—Natural History, No. 74955 *a*.)

Development of *Liparoceras cheltiense*.—The specimen examined was collected at the Battledown Pit, Charlton Kings, Cheltenham (Pl. XXI, figs. 4 *a*–4 *d*). The innermost whorls are not preserved, but at a diameter of 10 mm. the shell is quite smooth, the whorl being stouter and the form more involute than in the adult. The whorl thickness is equal to nearly three-quarters of the diameter until a much later stage; it is interesting to note that this condition is lost in *L. sparsicosta* at a diameter of 1 mm. In *L. cheltiense* there is a gradual change from the young to the adult form of whorl.

Fine tubercles are seen at a diameter of 10 mm.; they are already unpaired and are united by very feeble ribs which cross the venter (Pl. XXI, figs. 4 *c* & 4 *d*). Faint longitudinal striation is also present.[1] The young suture is more complicated than that of *L. sparsicosta*; for example, the suture of *L. cheltiense* at 8 mm. diameter has the first lateral lobe nearly as deep as the external lobe, a condition which is not attained by *L. sparsicosta* until much later.

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
70 mm.	48 per cent.	56 per cent.	20 per cent.
38	50	70	19
25	50	72	—
13	54	73	15

Young specimens of *L. cheltiense* (up to a diameter of 30 mm.) bear a superficial resemblance to *Becheiceras bechei*. They may be distinguished by their sutures (even at this diameter the first lateral lobe of *B. bechei* is deeper than the external lobe) and by the more depressed whorl of *L. cheltiense*; further, while tubercles

[1] Compare *A. striatus* Quenstedt, 'Petrefactenkunde Deutschlands : Cephalopoden' vol. i (1849) p. 135 & pl. ix, fig. 24.

appear in the young of *Liparoceras cheltiense* at a diameter of 10 mm., they are not present in *B. bechei* until twice that diameter.

Other specimens found at Battledown, apparently of this same lineage, show post-*cheltiense* stages in which the whorl is more slender, the ornament finer, and the tubercles generally paired. This latter character distinguishes *L. cheltiense* from the finely-ornamented sphærocones of the *Becheiceras* series.

LIPAROCERAS ZIETENI (Quenstedt).

Ammonites striatus zieteni Quenstedt (4, pl. xxviii, figs. 1 & 2).

Dimensions of figure :—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
64 mm.	50 per cent.	64 per cent.	22 per cent.

This presents a similar stage to *L. obtusinodum*, but differs in the greater arch of the periphery.

LIPAROCERAS HEPTANGULARE (Young & Bird).

(Refigured, 1, vol. ii, No. 108.)

This ammonite has a more slender whorl than *L. cheltiense*; the strongly-arched periphery may indicate a connexion with *L. zieteni*.

LIPAROCERAS TIARA, sp. nov. (Pl. XXI, figs. 1 *a* & 1 *b*; text-fig. 4 *d*, p. 270.)

Compare *Ammonites henleyi* A. d'Orbigny (3, pl. lxxxiii).

Dimensions of holotype :—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
63 mm.	41 per cent.	57 per cent.	29 per cent.

Stout whorl, evolute, with prominent unpaired tubercles (20/14) united by strong folds, dividing at the outer tubercles into two or three flattened ribs which cross the periphery.

Irregular longitudinal striation very marked.

Suture has a deep external lobe, divided by a high median saddle; first lateral lobe wide. Sutural elements very deeply undercut (text-fig. 4 *d*, p. 270).

This species, undoubtedly a Liparoceratid, differs from those previously considered in combining coarse ornament with an evolute form and very complex sutures.

The type-specimen was collected by Mr. L. Richardson in the Yellow Lias (hemera of *Beaniceras*), during excavations for a bridge at Manor Farm, Gotherington, near Cheltenham.

LIPAROCERAS PSEUDOSTRIATUM, sp. nov. (Fig. 4 *f*, p. 270.)

Compare *Ægoceras striatum* Wright (8, pl. xlii, figs. 1 & 3).

Dimensions of type-specimen :—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
100 mm.	47 per cent.	65 per cent.	16 per cent.

Differs from other species of *Liparoceras* in having stout whorls and involute form accompanied by unpaired fine tubercles.

Occurrence.—Upper part of the *ibex* zone, Dorset.

L. pseudostriatum is similar in appearance to *Androgynoceras divaricosta*, but has a stouter whorl, smaller umbilicus, unpaired tubercles, and more complicated suture of a different pattern.

The holotype is in the collection at University College, Cardiff.

B. Ægoceras.

Ægoceras aff. *latæcosta* (Sowerby). (Pl. XXIII, figs. 3 *a* & 3 *b*; text-fig. 5, p. 274.)

Compare *Ammonites latæcosta* Sowerby.[1]

Dimensions :—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
72 mm.	32 per cent.	33 per cent.	47 per cent.
50	30	30	46

Slender whorls little embracing, coiling regular; on the outer whorl are about thirty slightly-curved ribs, sharp on the sides and less prominent on the venter. On the last half-whorl, striæ are present between the ribs, especially on the venter. Feeble bituberculation commencing. Suture fairly complicated, external saddle very wide, first lateral lobe narrower and trifid, symmetrical. Collected by Dr. W. D. Lang (Coll. No. 1566) in the Lower Limestone (*latæcosta* sub-zone) of Dorset.

Development of *Ægoceras latæcosta*. (Pl. XXIII, figs. 4 *a*–4 *d*.)—The development was studied in a small specimen (W. D. Lang Coll. No. 534) from the *latæcosta* sub-zone (?), Stonebarrow. The young specimen, at a diameter of 14 mm., shows a body-chamber equal to half a whorl.

The protoconch is of normal form, preserved in calcite: an examination by transmitted light shows the so-called 'prosiphon' of Munier-Chalmas (Pl. XXIII, fig. 4 *d*). This structure is not always to be seen in ammonite protoconchs, owing to differences in preservation, and several investigators have failed to find any trace of it. Recently, however, Grandjean has shown it to be a solid structure extending from the end of the siphon to the inner wall of the protoconch.[2] The 'prosiphon' of *Ægoceras latæcosta* resembles the second type described by Grandjean, consisting of one long 'bandelette,' thus differing from *Æ. planicosta*, in which it is relatively short.

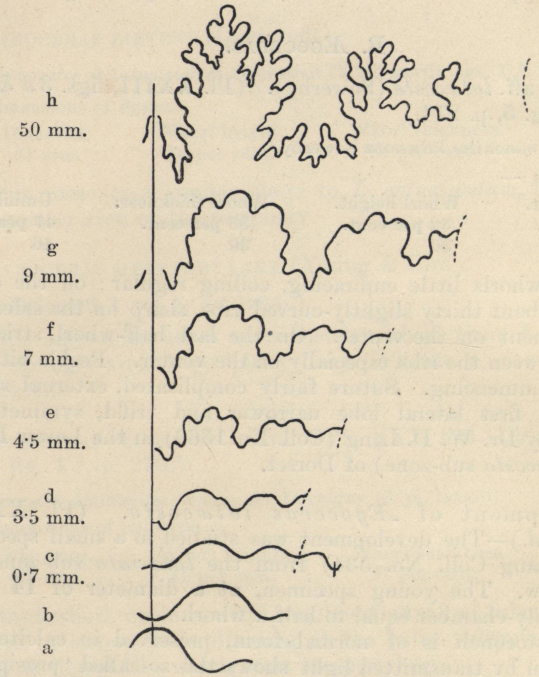
Shell-development proceeds normally, and, until *Æ. latæcosta* attains a diameter of over a millimetre, it is scarcely to be distinguished from other young capricorns. At a diameter of 4 mm. (Pl. XXIII, fig. 4 *a*) the whorl height of *Æ. latæcosta* is less than

[1] 'Mineral Conchology' vol. vi (1829) pl. dlvi, fig. 1.

[2] F. Grandjean, 'Le Siphon des Ammonites, &c.' Bull. Soc. Géol. France, ser. 4, vol. x (1910) p. 496.

the whorl height of the capricorns of *Amblycoceras* and *Oistoceras* at the same diameter; the whorl shape, however, does not differ markedly from that of *Liparoceras sparsicosta* until the diameter

Fig. 5.—*Sutural development of* Ægoceras latæcosta (*Sowerby*).



[a–g, W. D. Lang Coll. (figured in Pl. XXIII, fig. 4).
h=Specimen figured in Pl. XXIII, fig. 3: W. D. Lang Coll. No. 1566.]

of 10 mm. is reached, when *Ægoceras latæcosta* is less depressed. Low folds appear at a diameter of 3·5 mm.; but there are no ribs on the periphery until the shell is nearly twice that size, only becoming fairly prominent at a diameter of 11 mm.

Diameter. mm.	Whorl height. per cent.	Whorl thickness. per cent.	Umbilicus. per cent.
·84	43	79	26
1·2	40	67	32
2·5	40	68	?40
4·2	35	67	52
8·0	35	50	40
14·0	29	36	46

The early sutures of the capricorn forms are similar; indeed, the

sutures from the third to the tenth are almost identical in each species, the second suture having a ventral lobe which becomes divided by a minute median saddle in the next suture (text-fig. 5 *c*, p. 274). The first signs of denticulations appear in *Ægoceras latæcosta* at a diameter of 3·5 mm. and by 4·5 mm. the external saddle has three unequal terminal cells; the relatively-small first lateral lobe is feebly trifid (text-fig. 5*d*, *e*, p. 274). This lobe remains narrower than the external saddle but becomes deeper, and is as deep as the external lobe by the time that a diameter of 9 mm. is attained. The features of the suture may now be said to have reached the proportions characteristic of the adult.

In many young examples of this species the suture is tilted; that is to say, the saddles of one side are in advance of those of the other. If, therefore, only one side of such a specimen is examined, its sutures appear to resemble those of either *Amblycoceras* or *Becheiceras*.

ÆGOCERAS ÆQUICOSTA, sp. nov

Compare *Ægoceras maculatum* Wright (8, pl. xxxiv, figs. 1 & 3).

Dimensions of holotype:—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
70 mm.	28 per cent.	26 per cent.	45 per cent.

Whorl slender, almost circular in section, with uniformly-spaced ribs, little diminished on the periphery, which they cross without any curve. Thirty ribs on the outer whorl, where they are rounded; the ribs of the inner whorls, like those of *Æ. latæcosta*, are more acute. Suture of typical *Ægoceras* form, with large external saddle and narrow first lateral lobe.

Ægoceras æquicosta is proposed to include the English ammonites which were formerly called *Ammonites capricornus* Schlotheim, a name which is not used here, since its precise application is not known.

Occurrence.—Type-specimen, from the *latæcosta* sub-zone of Lincoln.

Ægoceras æquicosta differs from other capricorns in

(1) Nearly round whorl (the outer whorl of *Æ. latæcosta* is more elevated).

(2) Ribs very little diminished on the periphery (distinguishing it from most capricorns without a peripheral rib-curve).

With *Ægoceras æquicosta* at Lincoln occur specimens which show a catagenetic subcostate-striate stage.

In the *latæcosta* sub-zone of Dorset Dr. Lang has found ammonites, presumably of this lineage, which show a more advanced stage, resembling *A. henleyi* Sowerby in the moderately-round whorl, with flattened sides, and it is suggested that these ammonites (W. D. L. Coll. No. 3861) are intermediate between *Æ. latæcosta* and *Æ. dædalicosta*. They have swollen whorls,

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moderately wide umbilicus, just becoming imparinode, and show the irregular costæ seen in *Ægoceras dædalicosta*.

Dimensions of W. D. L. Coll. No. 3861 :—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
80 mm.	46 per cent.	57 per cent.	25 per cent.
47	44	51	25

These specimens are morphic equivalents of *Androgynoceras divaricosta*, from which they differ in the greater symmetry of the first lateral lobe (text-fig. 6, below) which resembles that of *Ægoceras latæcosta*.

ÆGOCERAS DÆDALICOSTA, sp. nov. (Pl. XXII, figs. 3 *a* & 3 *b*.)

Dimensions of holotype :—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
?190 mm.	50 per cent.	47 per cent.	13 per cent.

Whorl rounded, periphery arched, sides flattened, umbilicus small. Ribs irregular, especially on the venter, where they occasionally

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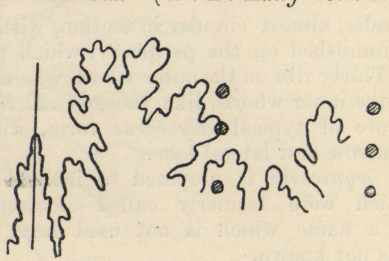
Fig. 6.—*Suture of* Ægoceras *sp., intermediate between* Æ. latæcosta *and* Æ. dædalicosta. *(W. D. Lang Coll. No. 3861.)*



show small but distinct bends ; they divide sometimes on the lateral area, and do not always unite with the outer tubercles. Tubercles distinctly unpaired (about 7/4 on a quarter of a whorl). The suture has the proportions characteristic of the genus ; the lobules of the first lateral lobe are practically equal in length, a feature shown by *Ægoceras latæcosta*.

There is very little trace of longitudinal striation on the outer whorl ; at a diameter of 40 mm. the ornamentation is finer and more regular, and striation is well-marked.

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The type-specimen was collected by Dr. Lang in the Red Band (*dædalicosta* sub-zone), St. Gabriel's Water, Dorset (No. 3862).

Æ. dædalicosta differs from other species of *Ægoceras* in having markedly unpaired tubercles and greater involution. The young has fine paired tubercles until a diameter of 30 mm.

C. Androgynoceras.

Androgynoceras maculatum (Young & Bird).

Refigured by S. S. Buckman (1, vol. i, No. 45).
Non A. maculatum Wright (8, pl. xxxiv).
Non A. maculatum Quenstedt (4, pl. xxxiv).

Androgynoceras obtusicosta, sp. nov. (Pl. XXII, figs. 2*a* & 2*b*.)

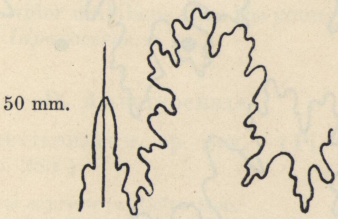
Compare *A. maculatum* (=*capricornum*) Wright (8, pl. xxxiv, figs. 4 & 5). *A. maculatum* Quenstedt (4, pl. xxxiv, fig. 5).

Dimensions of holotype :—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
80 mm.	34 per cent.	26 per cent.	46 per cent.

An evolute capricorn, bituberculation commencing. Whorl round up to a diameter of 50 mm., after which it becomes more elevated. Ribs pass directly across the venter and are very little diminished;

Fig. 7.—*Suture* of Androgynoceras obtusicosta (*Lincoln*).



round, 23 on the outer whorl, separated by wide spaces. Fine striæ between the ribs, especially on the periphery.

The suture shows a deep external lobe divided by a high median saddle; wide external saddles, first lateral lobes narrow and asymmetrically divided (text-fig. 7).

Occurrence.—*Latæcosta* sub-zone, Lincoln.

Distinguished from *Ægoceras latæcosta* by the suture and by the prominence of ribs on the periphery. With *A. obtusicosta* occur other ammonites in which the outer whorl is swollen, the capricorn stage commencing later and bituberculation earlier. These forms constitute a transition to *A. hybrida* (A. d'Orbigny).

Androgynoceras hybrida (A. d'Orbigny).

Ammonites hybrida d'Orbigny (3, pl. lxxxv, figs. 1–3, *non* figs. 4–5); compare *A. intracapricornus* Quenstedt (4, pl. xxix, fig. 9).

This is the *heterogenes*-stage of this series; its connexion with these ammonites is supported by the asymmetrical first lateral lobe and the proportions of the suture. The young figured by A. d'Orbigny probably is from a different ammonite, resembling *Oistoceras*.

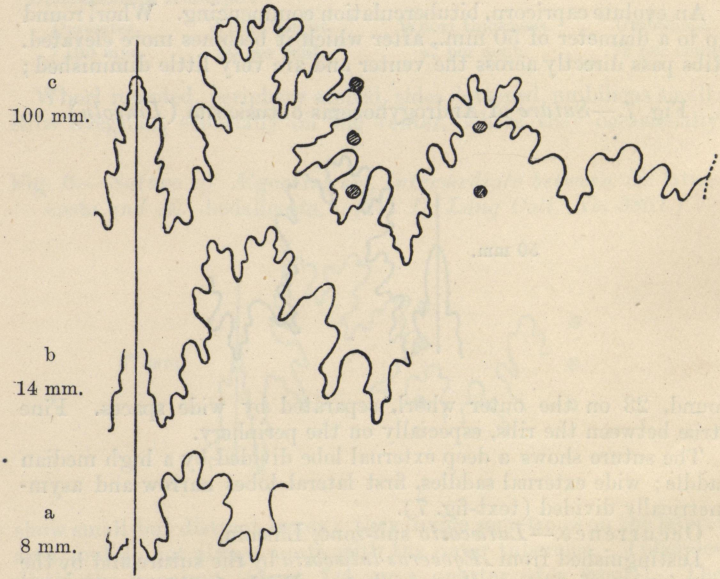
ANDROGYNOCERAS DIVARICOSTA, sp. nov. (Pl. XXII, figs. 1 *a*–1 *c* & text-fig. 8.)

Dimensions of holotype :—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
142 mm.	42 per cent.	57 per cent.	27 per cent.

Whorls swollen, nearly round, sides slightly flattened, moderately involute ; flattened costæ with two rows of tubercles. From the umbilical margin the ribs slope back to the inner tubercles ; between the tubercles they often divide, usually uniting again at the outer tubercles, splitting into two or three ribs which pass directly across

Fig. 8.—*Sutural development of* Androgynoceras divaricosta *(Lincoln)*.



the periphery. Tubercles usually paired, but the outer are slightly more numerous than the inner (imparinode stage commencing, 34/29).

The tubercles of the type-specimen are rounded knobs, but in specimens with a well-preserved shell they are moderately sharp. Longitudinal striations are present. Involution does not reach the inner row of tubercles.

Development.—The form of the shell throughout life changes very little, the whorls being nearly round and merely increasing in size. The shell is quite smooth up to a diameter of 4 mm., after which it has closely-set ribs for about a quarter of a whorl ; bituberculation commences at a diameter of 20 mm.

Diameter. mm.	Whorl height. per cent.	Whorl thickness. per cent.	Umbilicus. per cent.
14	43	50	—
22	46	52	—
50	48	54	27
120	48	56	30

Occurrence.—*Dædalicosta* sub-zone, Bracebridge and Waddington, near Lincoln (7, p. 104).

Androgynoceras divaricosta closely resembles specimens found in Dorset which are intermediate between *A. latæcosta* and *A. dædalicosta*, having a round whorl with slightly-flattened sides, tubercles nearly paired, and a moderately-wide umbilicus. The sutures indicate, however, that they belong to different series.

A. divaricosta has a superficial resemblance to *Liparoceras pseudostriatum*, from which it may be distinguished by

(1) Greater arch of the periphery and rounder whorl.

(2) Suture less complicated and having a large external saddle.

(3) The tubercles are only just becoming imparinode, and sometimes show longitudinal elongation. (Extension of tubercles in *Liparoceras* is usually, but not always, transverse.)

The young have a wider umbilicus than the young of sphærocones of *Becheiceras* and *Liparoceras*.

D. Amblycoceras.

Amblycoceras brevilobatum, sp. nov. (Pl. XXIV, fig. 3; text-fig. 10 *c*, p. 283.)

Holotype: *Liparoceras capricornu* Richardson.[1]
Compare *Amblycoceras capricornum* Hyatt.[2]
Compare *A. maculatum* Quenstedt, 4, pl. xxxiv, figs. 7–9.

Dimensions of holotype:—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
48 mm.	29 per cent.	27 per cent.	44 per cent.

A capricorn with elevated whorl and strong ribs, which are not much diminished on the periphery, where they curve forwards. The peripheral rib-curve is generally much less than that of *Oistoceras*, but often varies in individual specimens; thus some examples resemble *Oistoceras*, but are easily distinguishable by their sutural proportions. Sutures moderately complicated; first lateral lobe shallow and narrow, the ventral lobe has a broad median saddle, and the external saddle has three subequal terminal folioles (text-fig. 10 *c*, p. 283).

Development.—(Studied in specimens of *A. brevilobatum* from the Brick-Pit, Pilley, Leckhampton.)

The young forms in which the development was studied, had at

[1] L. Richardson, 'Geology of Cheltenham, &c.' 1904, pl. xv, fig. 7.

[2] A. Hyatt, in Eastman-Zittel, 'Text-book of Palæontology' 1st ed. vol. i (1900) p. 578, fig. 1204.

a diameter of 7 mm. a body-chamber already equal in length to more than three-quarters of a whorl. The inner whorls are smooth, and costæ are not acquired until the diameter of 3 mm. is reached. From this stage onwards the whorl becomes more elevated. Sutural development similar to that in *Amblycoceras crescens*, which will be next described: thus denticulations appear in each species at the same diameter and in the same order, and the sutures are remarkably similar (text-fig. 10 *b* & *c*, p. 283).

Diameter. mm.	Whorl height. per cent.	Whorl thickness. per cent.	Umbilicus. per cent.
0·7	50	75	—
1·4	43	55	35
3·0	42	60	33
4·7	40	51	32
7·5	37	40	33

Occurrence.—*Latæcosta* sub-zone, Brick-Pit, Pilley, Leckhampton.

Distinction: Suture and rib-curve distinguish *A. brevilobatum* from all species except *A. crescens*, which differs in having a stouter form.

With *A. brevilobatum* occur somewhat more advanced specimens having the outer whorl expanded, bituberculation commencing (S. S. Buckman Coll. No. 2817). This may be *Microceras sinuosum* Hyatt (2, p. 82), which is described as a bituberculate form with peripheral rib-curve; Mr. Buckman placed this species with *Oistoceras*,[1] but Hyatt refers to the shallow first lateral lobe of its suture, a character which suggests *Amblycoceras*.

AMBLYCOCERAS CRESCENS Hyatt. (Pl. XXIV, figs. 1*a*–1*b* & 2*a*–2*b*; text-figs. 9 & 10 *b*, pp. 281, 283.)

Compare *Ægoceras capricornum* Geyer.[2]

Dimensions of specimen figured here:—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
32 mm.	31 per cent.	34 per cent.	40 per cent.

A small capricorn, with stout thick whorls; ribs very prominent on the sides and periphery, where they have a forward bend. Ribs of the last whorl widely spaced (18 to the whorl).

Suture fairly simple; first lateral lobe very shallow; external lobe with broad and short median saddle (fig. 10 *b*, p. 283).

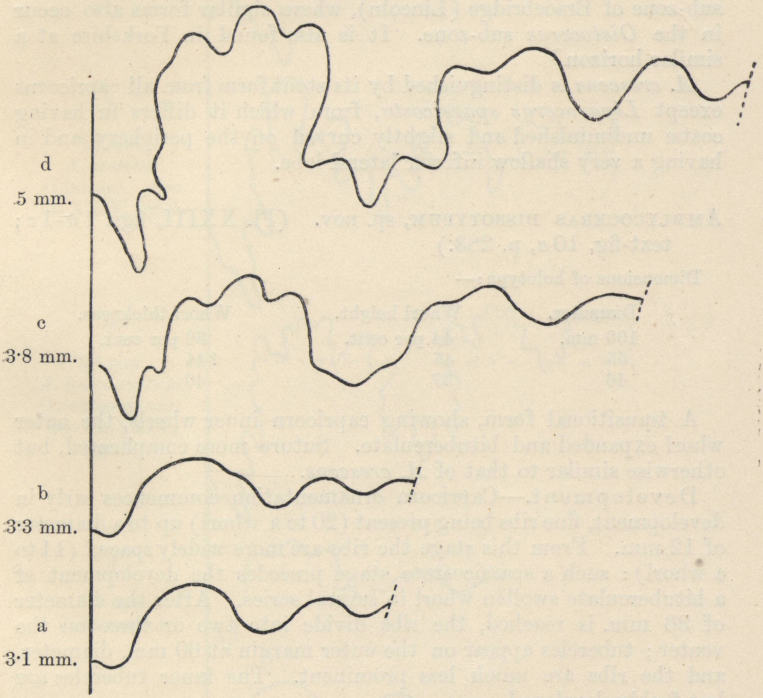
Hyatt named this species, but gave no figure; and the name has not been generally used. The specimen here figured agrees with Hyatt's description in having a shallow 'superior' lateral lobe and stout whorl.

[1] 'The Geology of the Country between Whitby & Scarborough' Mem. Geol. Surv. 2nd ed. (1915) p. 96.

[2] G. Geyer, 'Die Mittelliasische Cephalopoden-Fauna des Hinter-Schafberges in Ober-Œsterreich' Abhandl. K.-K. Geol. Reichsanst. vol. xv (1893) pt. 4, pl. iii, fig. 9.

Development (Pl. XXIV, figs. 2*a* & 2*b*).—Studied in a specimen from the *dædalicosta* sub-zone, Lincoln. The innermost whorls are not usually preserved; at a diameter of 2 mm. the shell is smooth with a depressed whorl, ribs appearing as folds on the lateral area at a diameter of 3 mm. This condition continues until over a whorl later, when at a diameter of 7 mm. faint folds cross the periphery with a decided forward curve. The whorl height has increased meanwhile, so that the whorl is almost circular in section; *A. crescens*, from this diameter onwards, is much stouter than any

Fig. 9.—*Sutural development of* Amblycoceras crescens (*Lincoln*).



other capricorn described. The ribs are regular and closely placed, until a diameter of 20 mm. (25 to a whorl), after which they are separated by wider spaces (18 to a whorl). The arrangement of the ribs on the inner whorls thus resembles that in *A. brevilobatum*.

Diameter. mm.	Whorl height. per cent.	Whorl thickness. per cent.
2	45	64
3·8	43	60
11	39	43
42	36	38

The suture at a diameter of 2 mm. has already a median ventral saddle, and the second lateral saddle is present as a low fold near the umbilical line (text-fig. 9 *a*, p. 281). The first denticulation of the suture appears on the dorsal margin of the external saddle at a diameter of 3·5 mm. A little later (after two sutures) the saddle is divided into three nearly equal terminal folioles (fig. 9 *b*). At the diameter of 3·8 mm. the first lateral lobe is feebly trifid, while the first lateral saddle has two unequal divisions (fig. 9 *c*). These features become more distinct in the next whorl: the second lateral saddle, though still undivided, is of greater size, and the first auxiliary is present.

Occurrence.—The specimens figured are from the *dædalicosta* sub-zone of Bracebridge (Lincoln), where similar forms also occur in the *Oistoceras* sub-zone. It is also found in Yorkshire at a similar horizon.[1]

A. crescens is distinguished by its stout form from all capricorns except *Liparoceras sparsicosta*, from which it differs in having costæ undiminished and slightly curved on the periphery and in having a very shallow inferior lateral lobe.

AMBLYCOCERAS DISSOTYPUM, sp. nov. (Pl. XXIII, figs. 1 *a*–1 *c*; text-fig. 10 *a*, p. 283.)

Dimensions of holotype:—

Diameter.	Whorl height.	Whorl thickness.
100 mm.	44 per cent.	36 per cent.
65	45	?44
46	37	40

A transitional form, showing capricorn inner whorls, the outer whorl expanded and bituberculate. Suture more complicated, but otherwise similar to that of *A. crescens*.

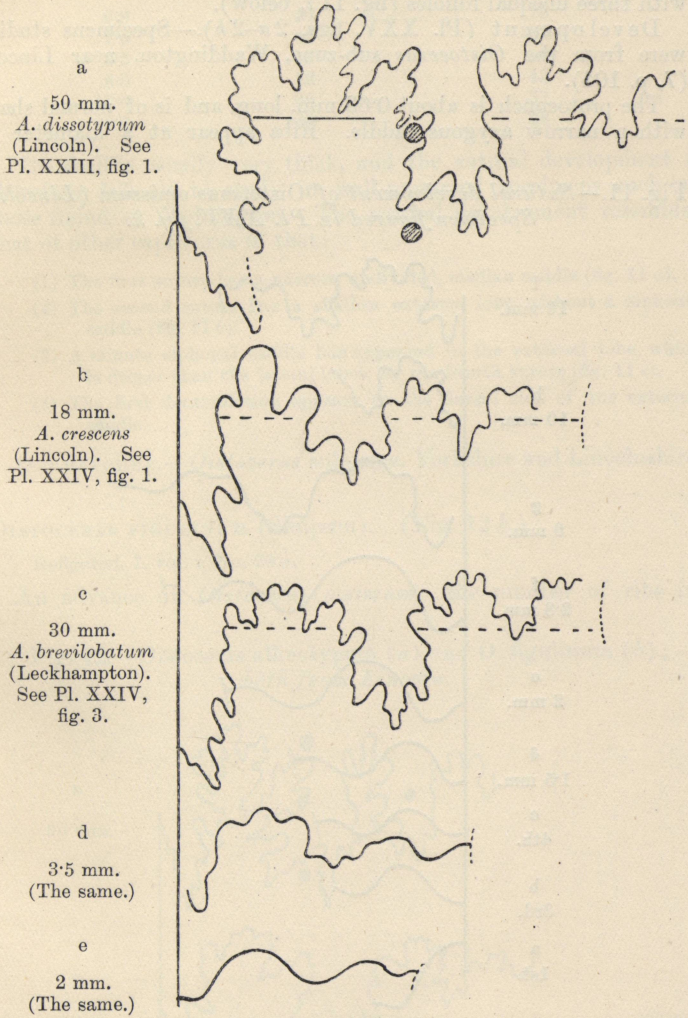
Development.—Capricorn ornamentation commences early in development, fine ribs being present (20 to a whorl) up to a diameter of 12 mm. From this stage the ribs are more widely spaced (14 to a whorl): such a sparsicostate stage precedes the development of a bituberculate swollen whorl in several series. After the diameter of 36 mm. is reached, the ribs divide into two or three on the venter; tubercles appear on the outer margin at 60 mm. diameter, and the ribs are much less prominent. The inner tubercles are but feebly developed.

The arrangement of costæ and the depressed shape of the inner whorls in this ammonite thus recall *A. crescens*, from which it presumably is derived.

Occurrence.—The type-specimen of *A. dissotypum* was collected in the *dædalicosta* sub-zone at Bracebridge, near Lincoln. It is distinguished from other Liparoceratids of this stage by its suture, with shallow first lateral lobe, and by its peripheral rib-curve.

[1] S. S. Buckman, 'Geology of the Country between Whitby & Scarborough' Mem. Geol. Surv. 2nd ed. (1915) p. 69.

Fig. 10.—*Sutures of* Amblycoceras *spp.*



E. Oistoceras.

Oistoceras omissum (Simpson). (Pl. XXV, figs. 2 *a*–2 *h*; text-fig. 11, p. 284.)

Refigured, 1, vol. i, No. 27.

Compare *A. maculatum angulatum* Quenstedt (4, pl. xxxiv, figs. 11 & 12).

Dimensions of figure (in 1, No. 27):—

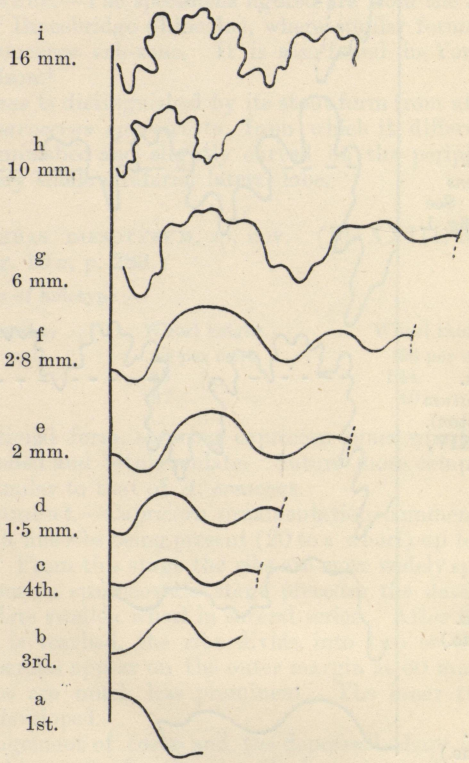
Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
28 mm.	25 per cent.	? 32 per cent.	54 per cent.

Suture simple; first lateral lobe narrow, external saddle wide with three unequal folioles (fig. 11 *i*, below).

Development (Pl. XXV, figs. 2 *a*–2 *h*).—Specimens studied were from the *Oistoceras* sub-zone, Waddington, near Lincoln (7, p. 104).

The protoconch is about 0·63 mm. long, and is of normal shape with a narrow azygous saddle. Ribs appear at a diameter of

Fig. 11.—*Sutural development of* Oistoceras omissum (*Lincoln*). *Specimen figured in Pl. XXV, fig. 2.*



2 mm. at the commencement of the second whorl, but do not cross the venter until a diameter of 9 mm. is reached. The ribs have an arrow-like forward projection on the periphery. Throughout development the ribs are fine and regularly spaced, the number of ribs to a whorl increasing steadily with growth; thus, at a diameter of 30 mm., there are usually thirty ribs on the last whorl. In some species (*Oistoceras figulinum*) the number becomes reduced in the adult or in old age.

Diameter. mm.	Whorl height. per cent.	Whorl thickness. per cent.
0·8	40	73
1·5	43	64
3·5	42	56
8·0	42	42
16·0	36	37
28·0	28	28

The shell is usually very thick, and the sutural development is therefore difficult to study in well-preserved specimens such as those found at Waddington. The sutural development resembles that of other capricorns in that:

(1) The first suture has a narrow, undivided, median saddle (fig. 11 *a*).
(2) The second suture has a shallow external lobe without a siphonal saddle (fig. 11 *b*).
(3) A minute siphonal saddle has appeared in the external lobe, which is deeper than the lateral lobes, by the fourth suture (fig. 11 *c*).
(4) The first denticulation appears on the dorsal side of the external saddle.

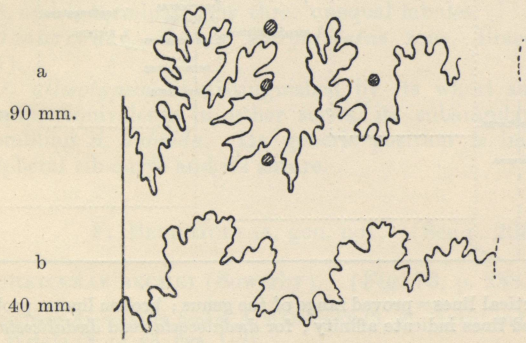
Occurrence.—*Oistoceras* sub-zone, Yorkshire and Lincolnshire.

OISTOCERAS FIGULINUM (Simpson). (Fig. 12 *b*.)

Refigured, 1, vol. i, No. 26 *a*.

An advance on *Oistoceras omissum*; the number of ribs on

Fig. 12.—Oistoceras allœotypum (*a*) *and* O. figulinum (*b*); *both from Lincoln.*



[a = Specimen figured in Pl. XXV, fig. 1.]

a whorl increases in early development, but the ribs of the last whorl are more widely spaced.

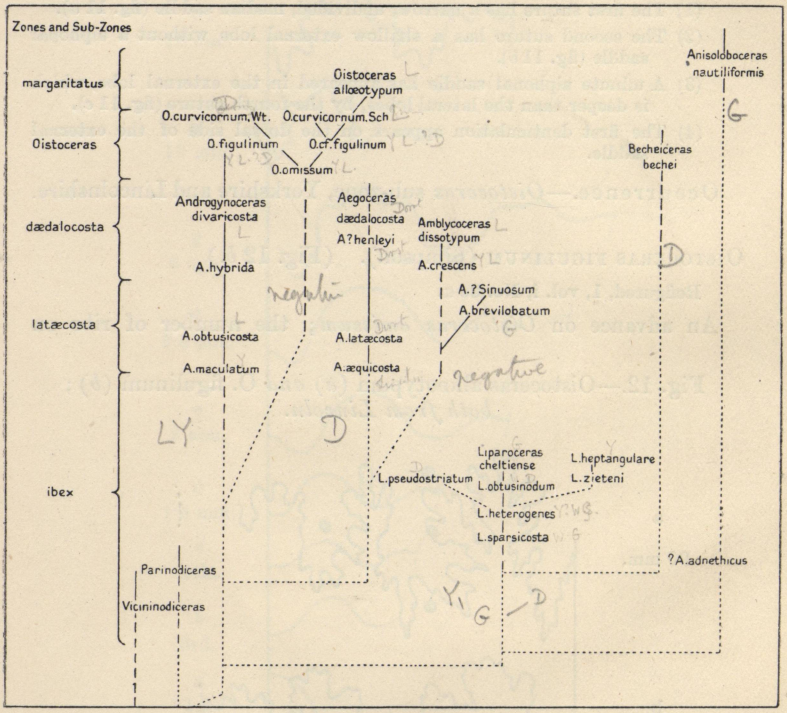
Occurrence.—*Oistoceras* sub-zone, Yorkshire, Lincolnshire, ? Dorset.

OISTOCERAS CURVICORNUM (Schlœnbach).

Ammonites curvicornis Schlœnbach, 'Ueber den Eisenstein des Mittleren Lias in Nord-West Deutschland, &c.' Zeitschr. Deutsch. Geol. Gesellsch. vol. xv (1863) p. 522 & pl. xii.

This differs from *A. curvicornum* Wright (8, pl. xxxi, figs. 3 & 4) in having a rounded venter, that of the latter being flattened. Wright's form has also more prominent tubercles. The probable relations of these species are shown in Table III.

TABLE III, *showing the probable relationships of the species of the Liparoceratidæ.*



[Continuous vertical lines = proved range of the genus; broken lines = probable range; dotted lines indicate affinity; for *dædalocosta* read *dædalicosta*.]

O. curvicornum (Schlœnbach *non* Wright) may be represented at Waddington, near Lincoln. The form figured by Wright occurs at a corresponding level (the *Oistoceras* sub-zone) in Dorset.

In each of these series three types may be distinguished:

(1) With peripheral costæ sharp and distinct.

(2) With a fold passing straight across the venter, the rib-curve being indicated by striations only.

(3) Without folds on the periphery; curved striations only.

It does not seem necessary at present to create new species for these forms.

OISTOCERAS ALLŒOTYPUM, sp. nov. (Pl. XXV, figs. 1 *a* & 1 *b*; text-fig. 12 *a*, p. 285).

Dimensions :—

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
90 mm.	40 per cent.	37 per cent.	38 per cent.
45	35	35	44

A *heterogenes*-like form (morphic equivalent of *Androgynoceras hybrida*) with capricorn ornament on the inner whorls, the last half of the outer whorl swollen and having more slender costæ and two rows of tubercles. The forward curve of the ribs on the periphery is clearly shown.

Capricorn ribs are retained until a diameter of 70 mm., when the shell is scarcely different from *O. figulinum*. The costæ are regular up to a diameter of 40 mm., after which they are more widely spaced. Two rows of tubercles are present on the outer whorl, but those of the inner row are very feeble. The ribs divide at the outer tubercles, passing with a sharp bend across the slightly-angular (convexi-fastigate) venter. Suture complex, but on the same plan as *Oistoceras omissum*; deep and narrow external lobe with a high median saddle, half as high as the external saddle. This latter is asymmetrically divided, being deeply undercut on the dorsal side. The first lateral lobe is nearly as deep as the external lobe, and is terminated by three unequal lobules.

Occurrence.—Lower *margaritatus* zone, Bracebridge (Lincoln).

O. allœotypum is distinguished by its whorl shape from its morphic equivalents in other series, its subangular venter most resembling *A. hybrida*. Its generic position is indicated by its peripheral rib-curve and its suture.

F. BECHEICERAS, gen. nov. (See p. 263.)

BECHEICERAS BECHEI (Sowerby). (Fig. 13, p. 288.)

Compare *Ammonites bechei* A. d'Orbigny (3, pl. lxxxii) and *Ægoceras bechei* Wright (8, pl. xli, figs. 1–2).

A. bechei, formerly considered by many workers to be synonymous with *A. striatus* or *A. henleyi*, has generally been applied in more recent years to the finely-ornamented sphærocones of several series of the Liparoceratidæ. The sutural characters pointed out (fig. 1 *b*, p. 258) restrict the name to ammonites of the *Becheiceras* series only.

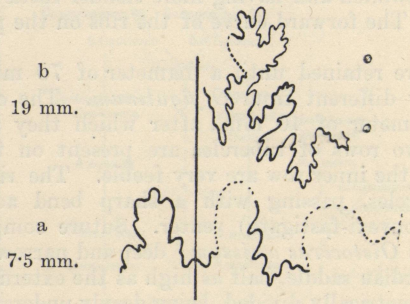
A typical example of *Becheiceras bechei* was obtained by Dr. Lang from the Upper Limestone (*Oistoceras* sub-zone) of Dorset (W. D. Lang Coll. No. 4073). This remains smooth until the diameter of nearly 20 mm., when it becomes finely bituberculate; the capricorn stage through which this series presumably passed is omitted in development.

There is, therefore, little change in whorl shape.

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
6 mm.	46 per cent.	67 per cent.	—
12	50	58	16 per cent.
28	56	56	11
41	53	53	—

C.202.44.

Fig. 13.—*Sutural development of* Becheiceras bechei *(W. D. Lang Coll. No. 4073).*



Ammonites which constitute an earlier stage in the *B. bechei* series occur in the *dædalicosta* sub-zone of Dorset; they have a somewhat wider umbilicus than *B. bechei.*

It has already been indicated that *B. bechei* is very similar to certain finely-ornamented forms in other series. The following points of distinction are useful:—

(1) The sutural proportions (text-fig. 1 *b*, p. 258).

(2) At all stages in development the whorl thickness of *B. bechei* is less than in corresponding stages of *Liparoceras.*

(3) The young of *B. bechei* is smooth for a longer period than the young of other forms.

G. Parinodiceras, gen. nov. (See p. 264.)

Parinodiceras reineckii (Quenstedt) (4, pl. xxviii, fig. 5).

A compressed sphærocone with smooth inner whorls (no capricorn stage). Bituberculate, tubercles paired, regular, nearly forty in each row, the two rows widely separated. The ribs do not divide on the lateral area, but divide into two or three on the

periphery, where they are very prominent. No longitudinal striations visible. Suture complex; external lobe deep and narrow, with a high median saddle, external saddle high, not extending quite to the outer row of tubercles, first lateral lobe a little deeper than the external lobe. This species differs from *P. parinodum* (Quenstedt) 4, pl. xxviii, figs. 16–17, in the greater arch of the periphery.

A typical specimen in the collection of Mr. Buckman (No. 2098), from Radstock, Somerset (*valdani* zone), has the dimensions:

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
140 mm.	60 per cent.	39 per cent.	9 per cent.

H. Vicininodiceras, gen. nov. (See p. 264.)

Vicininodiceras simplicicosta, sp. nov. (Pl. XXIV, figs. 4 *a* & 4 *b*.)

Diameter.	Whorl height.	Whorl thickness.	Umbilicus.
87 mm.	51 per cent.	58 per cent.	20 per cent.

A bituberculate sphærocone; whorls round, inner whorls smooth (no capricorn stage). Tubercles paired, at wide intervals on the outer whorl (about twenty in each row); the two rows very close together, the inner row being high up on the whorl. Ribs simple, annular, with a faint backward curve on the periphery, not dividing at the tubercles; only about a sixth of the ribs of the outer whorl bear tubercles. Except in one case the tubercles are broken off; they are longitudinally elongated, and appear to be placed on one rib, touching the ribs on each side.

Suture very complicated, with a deep external lobe and high median saddle, the first lateral lobe wide and slightly deeper than the external lobe; the whole of the external saddles and part of the first lateral lobe are ventral to the outer row of tubercles.

V. simplicicosta is distinguished by its paired tubercles from all Liparoceratids, except *Parinodiceras* and *A. striatus* Reinecke, from both of which it differs in having undivided ribs and the tubercles placed close together; it is further distinguished by the form of the whorl.

Only three specimens of this ammonite have been examined; they are in the collection of Mr. J. W. Tutcher, who obtained them at Radstock, Somerset (*valdani* zone).

VII. Phylogeny and General Considerations.

Early Capricorn Forms.

Although the capricorns of the Liparoceratidæ are most abundant in the *davœi* zone, yet more primitive capricorns have been found as low as the *oxynotum* and *raricostatum* zones. Two such forms

have been described as *Androgynoceras siphunculare* and *A. integricostatum*, which occur in the *gagateus* band (*oxynotum* zone) of Robin Hood's Bay. These ammonites are smooth until a diameter of 3 mm., and their sutures are simpler than those of the later forms at corresponding diameters.[1]

The species figured by Reynès (6, pl. l, figs. 26–32, pl. xlv, figs. 47–49) from the *raricostatum* zone (*A. sirius* and *A. vesta*) are very little more advanced than these forms. *A. circumdatus* Reynès (6, pl. xxviii, figs. 19–22) described from the *bucklandi* zone and placed by Mr. Buckman on the line of descent of the capricorns,[2] is probably a member of another series, and cannot be considered as the early ancestor of the Liparoceratidæ; but it may represent an offshoot from their ancestral stock.

It is probable, however, that the capricorn forms possessed their essential characters at a comparatively early date; thereafter evolution proceeded slowly for some time, and consisted solely in the acceleration of the capricorn ornament and the increase of complication of the sutures. The development of bituberculation and the sphærocone form in each series was comparatively sudden; this period of rapid evolution appears to have frequently followed the arrival of a series in this area.

The Pre-Capricorn Ancestor.

It has been shown that the inner whorls of the Liparoceratidæ are invariably smooth and depressed, with a relatively-narrow umbilicus; the young of many ammonites of various families have a similar form. Prof. J. Perrin Smith has suggested[3] that the *Glyphioceras*-like young may be explained in two ways:—

(1) They may indicate that all ammonites are descended from a *Glyphioceras*-like ancestor.

(2) This form of shell may be cœnogenetic and not palingenetic; that is, it may be acquired owing to its suitability during the early life of all ammonites, and may have no reference to the form of the ancestor.

In support of the latter view it may be mentioned that the protoconch of every ammonite has a depressed form of aperture; it is, therefore, probable that the succeeding whorls will gradually become more elevated until they attain the adult shape. That is to say, the depressed inner whorls may be a result of the form of the protoconch, and may be independent of the form of the ancestor.

[1] Thus the suture of *A. siphunculare* (Whitby Museum, No. 485) at a diameter of 20 mm. has an external saddle divided simply into three terminal folioles, and a first lateral lobe with three small lobules, a stage which is attained by the suture of the capricorns described previously at a much smaller diameter (figs. 2 *e*, 9 *d*, 11 *g*, pp. 266, 281, 284).

[2] S. S. Buckman, Q. J. G. S. vol. liv (1898) table ii, facing p. 451.

[3] 'Acceleration of Development in Fossil Cephalopods' Stanford Junior University Publications, 1914.

The former view has been maintained by Mr. Buckman,[1] who suggested that *Cymbites* is the ancestor of many Mesozoic ammonites; the inner whorls of ammonites are remarkably similar in form to those of the adult *Cymbites*, but also the sutural development of many ammonites suggests that they arose from a *Cymbites*-like ancestor. It must further be noticed that there are numerous transitional forms which appear to connect globose (*Glyphioceras*-like) species with ammonites of many families,[2] a fact which appears to indicate the truth of Mr. Buckman's suggestion, but cannot easily be reconciled with the second view put forward by Prof. J. P. Smith.[3]

These globose ammonites have generally been called *Cymbites globosus*: the name has probably been used, however, to cover several species which differ little in outward form, but have a long vertical range[4]; from this central group the various ammonite-families may have arisen at different times.

The Triassic ancestor of *Cymbites* (and so, perhaps, of most Jurassic ammonites) is probably an involute form, with a depressed whorl and simple suture comprised of few elements. Mr. Buckman suggested that *Nannites* may be the ancestral form[5]; but, as this acquires constrictions in the adult,[6] which are not reproduced in *Cymbites*, it is probably only safe to assume that it is near the line of descent of the ammonites.

General Considerations.

A genealogy of Jurassic ammonites was given by Mr. Buckman in 1898.[7] Since that date his own views have undergone considerable modification, and it must be stated that some of the differences between that genealogy and the one given here have been suggested to me by Mr. Buckman's subsequent writings.

[1] 'On the Genus *Cymbites*' Geol. Mag. dec. 4, vol. i (1894) p. 360.

[2] For example, in the nodules of the *planicosta* sub-zone of Dorset the following series may be found:

(1) *Cymbites* sp. of the *C.-lævigatus* pattern, more evolute than *C. globosus*.
(2) *Cymbites* sp. of the *C. berardi* pattern, with broad lateral costæ and smooth periphery.
(3) Ammonites with broad costæ, which pass across the periphery.
(4) Ammonites of the *planicosta* group, frequently smooth up to a diameter of 8 mm.

[3] If the 'skipping of stages' demonstrated in this paper has been of frequent occurrence, it may often prove impossible to judge ancestry from ontogenetic evidence, and the tracing of numerous connecting forms will be necessary in determining genealogies.

[4] Thus the sutural development of examples from the Middle Lias proceeds more rapidly than that of specimens from the Lower Lias.

[5] *Op. supra cit.* 1894, p. 360.

[6] A. Hyatt & J. P. Smith, 'Triassic Cephalopod Genera of America' U.S. Geol. Surv. Prof. Paper, No. 40 (1905) p. 78.

[7] S. S. Buckman, 'Divisions of so-called Jurassic Time' Q. J. G. S. vol. liv (1898) table ii, facing p. 451.

The early evolution of the Echioceratidæ and the Liparoceratidæ is parallel, both families developing capricorn ornamentation at approximately the same time. In subsequent evolution, however, while the Liparoceratidæ become expanded and bituberculate, the Echioceratidæ always remain slender, never develop bituberculation, and in later stages acquire a carina. Although the early evolution of the two families was parallel, separation must have occurred at a comparatively early date, for the sutures, even in the young forms, are very distinct.

It is extremely probable that the Hildoceratidæ arose from a similar stock at a later date; the early evolution resembles that of the Echioceratidæ and the sutures are similar, but the carina becomes more prominent. The Hildoceratidæ may comprise several parallel lines of descent from a *globosus*-like form. Some specimens of *Frechiella*, a globose ammonite with keeled venter (1, vol. i, No. 23), have typical Hildoceratan sutures and may be intermediate between the ancestral form and one of the later branches of the Hildoceratidæ.

It seems probable, therefore, that the Liparoceratidæ, Echioceratidæ, Hildoceratidæ, Polymorphidæ,[1] and Deroceratidæ [2] may have developed directly from a globose ancestor. Other families, however, while they have probably descended from a similar globose form, have passed through a subsequent cadicone stage; thus Hyatt[3] regarded *Cœloceras pettos*, a broad-ventered (cadicone) tuberculate ammonite, as the acmic tertiary radical of the Dactyloidæ. Some members of the Dactyloidæ pass through a *pettos*-like stage with cadicone whorls and smooth venter.[4] Later Dactyliocerates omit the cadicone stage altogether in development, an omission which is comparable with the skipping of the capricorn stage in the development of the later Liparoceratidæ.

The *Beaniceras* series, to which reference has already been made, passes from a tuberculate cadicone to a capricorn, similar in outward appearance to the anagenetic capricorns of the Liparoceratidæ. Mr. S. S. Buckman, who placed *Beaniceras* with the Liparoceratidæ (1, vol. ii, p. *iii*), now agrees with me that its affinities are with the Dactyloids, which it resembles in sutural characters and in the cadicone ancestry.

The Amaltheidæ likewise pass through a cadicone stage, and may perhaps be considered as related to the Dactyloids rather than,

[1] A. E. Trueman, 'Observations on the Genus *Polymorphites*' Geol. Mag. dec. 6, vol. iv (1917) p. 442.

[2] The Deroceratidæ have sutural characters (particularly a deep suspensive auxiliary lobe) which separate them from the greater part of the Lias Ammonites.

[3] A. Hyatt, 'The Genesis of the Arietidæ' Smithsonian Contributions to Knowledge, No. 673 (1889) p. 23. See also A. Hyatt, 'The Non-Reversionary Series of the Liparoceratidæ, &c.' Proc. Bost. Soc. Nat. Hist. vol. xv (1872–73) p. 4.

[4] *Cœloceras fonticulum* has a *pettos*-like stage from the diameter of 5 mm. to that of 10 mm. After this stage ribs appear on the venter. Some species of *Porpoceras* and *Peronoceras* show corresponding stages.

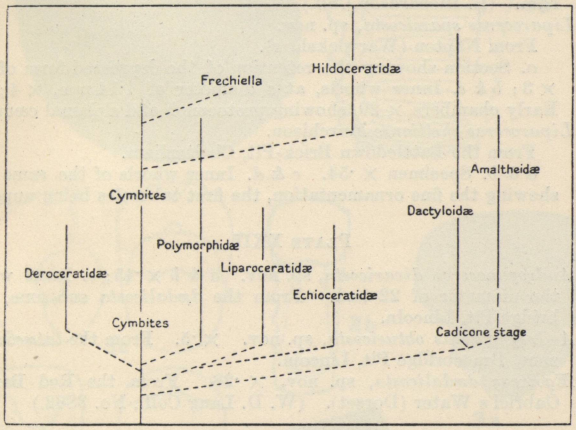
as Mr. Buckman suggested, to the Liparoceratidæ (1, vol. ii, p. *vii*).

That is to say, two main groups of ammonites may be recognized in the families mentioned :—

(1) Those which evolved directly from a globose ancestor (Liparoceratidæ, Hildoceratidæ, Polymorphidæ, Echioceratidæ, Deroceratidæ).

(2) Those which have passed through an intermediate cadicone stage (Amaltheidæ, Dactyloidæ). (See Table IV, below.)[1]

TABLE IV.—*Diagram showing the possible relationships of the chief Liassic families of Ammonites.*



It is interesting to note that a carinate venter is acquired independently in several families of each of these groups, typically in the Hildoceratidæ and Amaltheidæ, less prominently in the Echioceratidæ and the Polymorphidæ and in some members of the Deroceratidæ. The development of a carina is a normal progressive feature; and, while it leads to a certain similarity between some forms, it does not necessarily imply any close relationship.

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[1] It does not necessarily follow, however, that the cadicone form of whorl has not been developed in groups that are unrelated.

EXPLANATION OF PLATES XXI–XXV.

[All the specimens, except where otherwise stated, were collected by the Author, and are now in the collection of the Geological Department, University College, Nottingham.]

Plate XXI.

Fig. 1. *Liparoceras tiara*, sp. nov. × ·8.
Yellow Lias (hemera of *Beaniceras*), collected during excavations for a bridge near Manor Farm, Gotherington, Cheltenham. (L. Richardson Coll.)

2. *Liparoceras sparsicosta*, sp. nov. × ·7.
From a well at Queen's Wood cottages, Prestbury, near Cheltenham. (L. Richardson Coll.)

3. *Liparoceras sparsicosta*, sp. nov.
From Napton (Warwickshire).
a. Section showing the retention of the depressed form of whorl × 3; *b* & *c*. Inner whorls, at a diameter of 1·14 mm. × 4; *d* & *e*. Early chambers × 20, showing protoconch and siphonal cæcum.

4. *Liparoceras cheltiense* Murchison.
From the Battledown Brick-Pit, Cheltenham.
a & *b*. Specimen × ·54. *c* & *d*. Inner whorls of the same × 1·6, showing the fine ornamentation, the first tubercles being unpaired.

Plate XXII.

Fig. 1. *Androgynoceras divaricosta*, sp. nov. *a* & *b* × ·45; *c*. Inner whorl at the diameter of 22 mm. From the *dædalicosta* sub-zone, Bracebridge Pit, Lincoln.

2. *Androgynoceras obtusicosta*, sp. nov. × ·5. From the *latæcosta* sub-zone, Bracebridge Pit, Lincoln.

C. 20231. 3. *Ægoceras dædalicosta*, sp. nov. × ·28. From the Red Band, St. Gabriel's Water (Dorset). (W. D. Lang Coll., No. 3862.)

Plate XXIII.

Fig. 1. *Amblycoceras dissotypum*, sp. nov. *a* & *b* × ·6; *c* = Whorl shape at the diameter of 44 mm. From the *dædalicosta* sub-zone, Bracebridge Pit, Lincoln.

2. *Beaniceras* sp. Inner whorls. × 2·5. From Napton (Warwickshire). (C. H. Watson Coll.)

C. 20233. 3. *Ægoceras* aff. *latæcosta* Sowerby. *a* × ·4; *b* = Whorl shape × ·8. From the Lower Limestone, *latæcosta* sub-zone, Dorset. (W. L. Lang Coll., No. 1566.)

C. 20234 4. *Ægoceras* aff. *latæcosta*, development. *a*, *b*, & *c*. Inner whorls at the respective diameters of 1·4 mm., ·95 mm., ·7 mm.; *d*. Earlier chambers, showing 'prosiphon,' × 20. From the (?) *latæcosta* sub-zone, Stonebarrow (Dorset). (W. D. Lang Coll., No. 534.)

Plate XXIV.

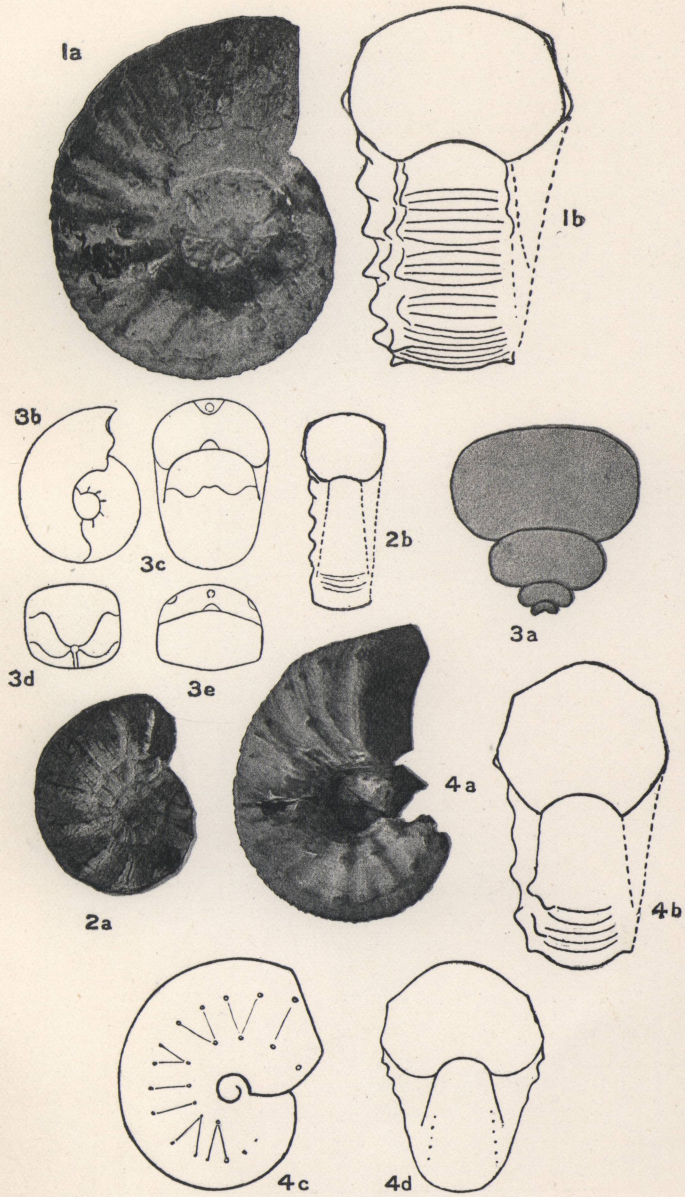
Fig. 1. *Amblycoceras crescens* (Hyatt). × ·73. From the *dædalicosta* sub-zone, Bracebridge, near Lincoln.

2. The same. Inner whorls at the diameter of 3·7 mm. × 11.

3. *Amblycoceras brevilobatum*, sp. nov. × 6·5. Front view of holotype, figured by Mr. L. Richardson (in 'The Geology of Cheltenham, &c.' 1904, pl. xv, fig. 7).

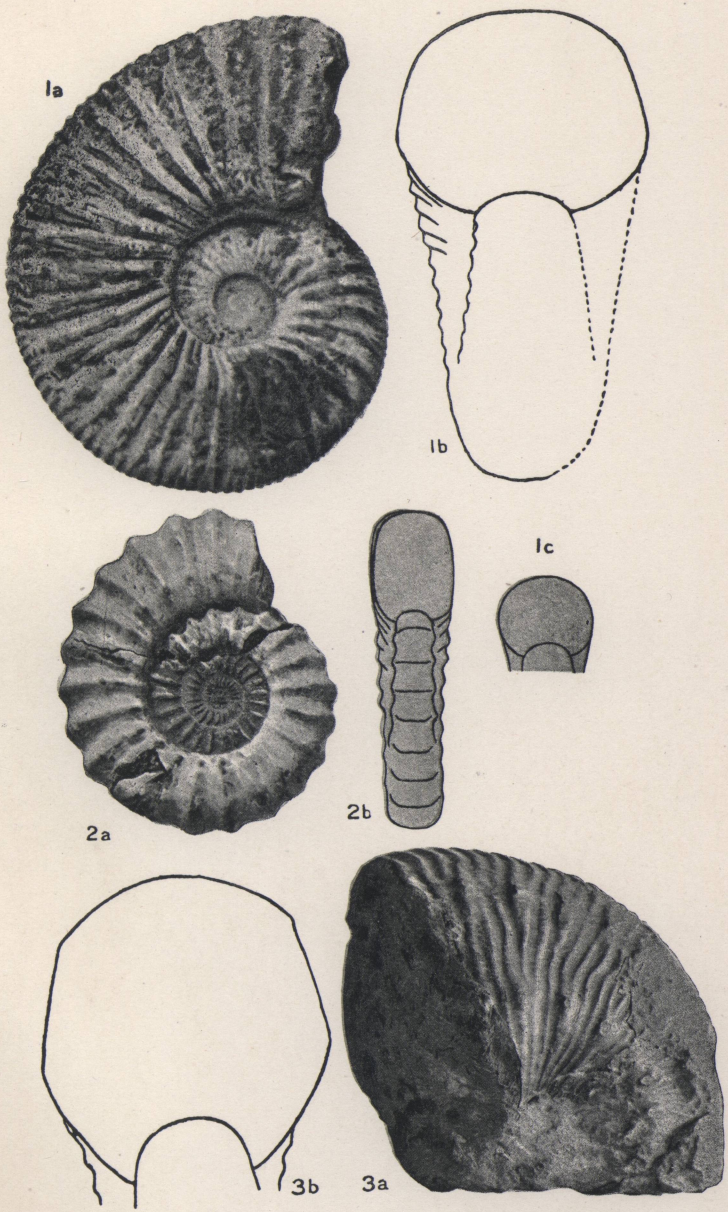
4. *Vicininodiceras simplicicosta*, sp. nov. × ·65. From the '*valdani*-zone,' Radstock (Somerset). (J. W. Tutcher Coll.)

5. *Cymbites* sp. From the *planicosta* sub-zone, Lyme Regis (Dorset). Sections of inner whorls. *a*, × 4; *b*, × 20.



A. E. T. del. et photo

LIPAROCERAS.



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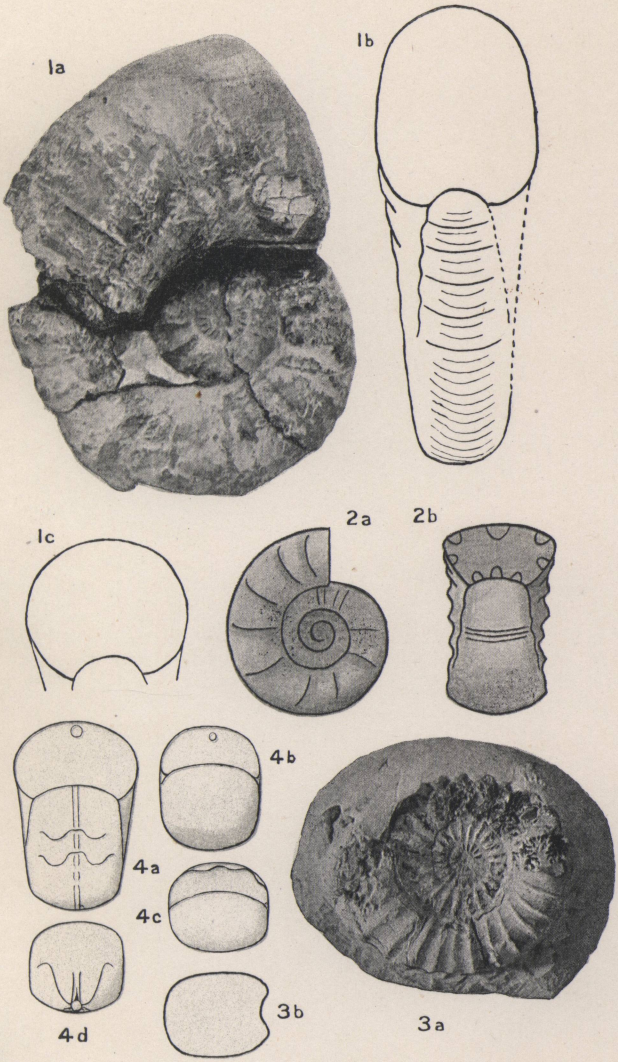
ANDROGYNOCERAS, ÆGOCERAS.



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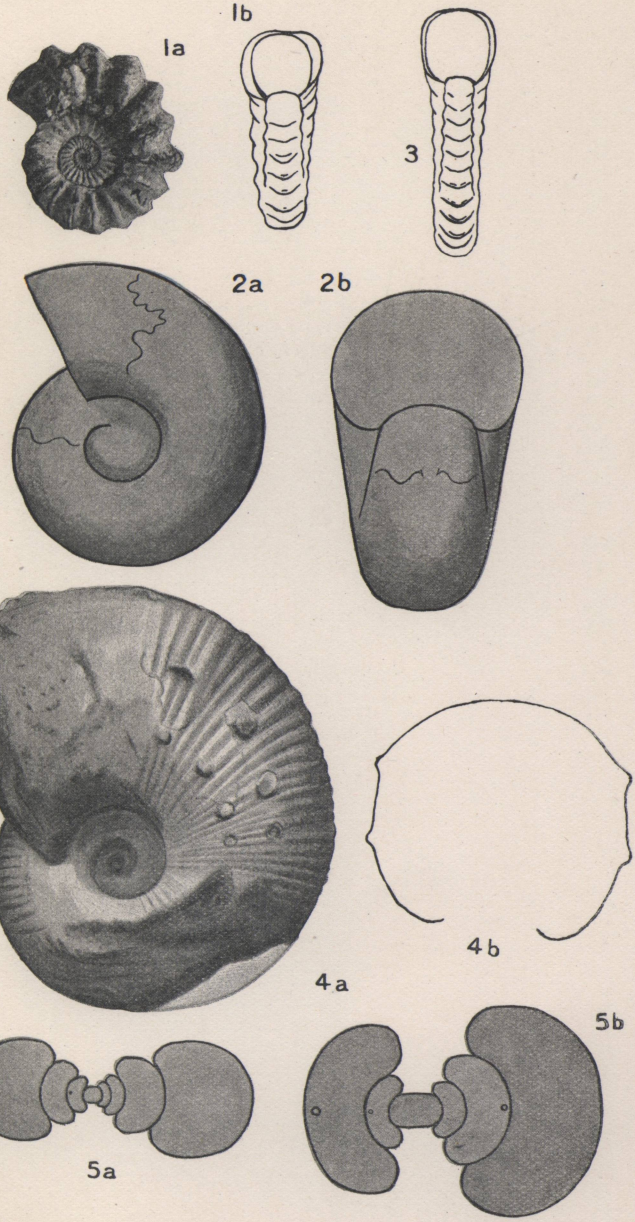
AMBLYCOCERAS, BEANICERAS, ÆGOCERAS.



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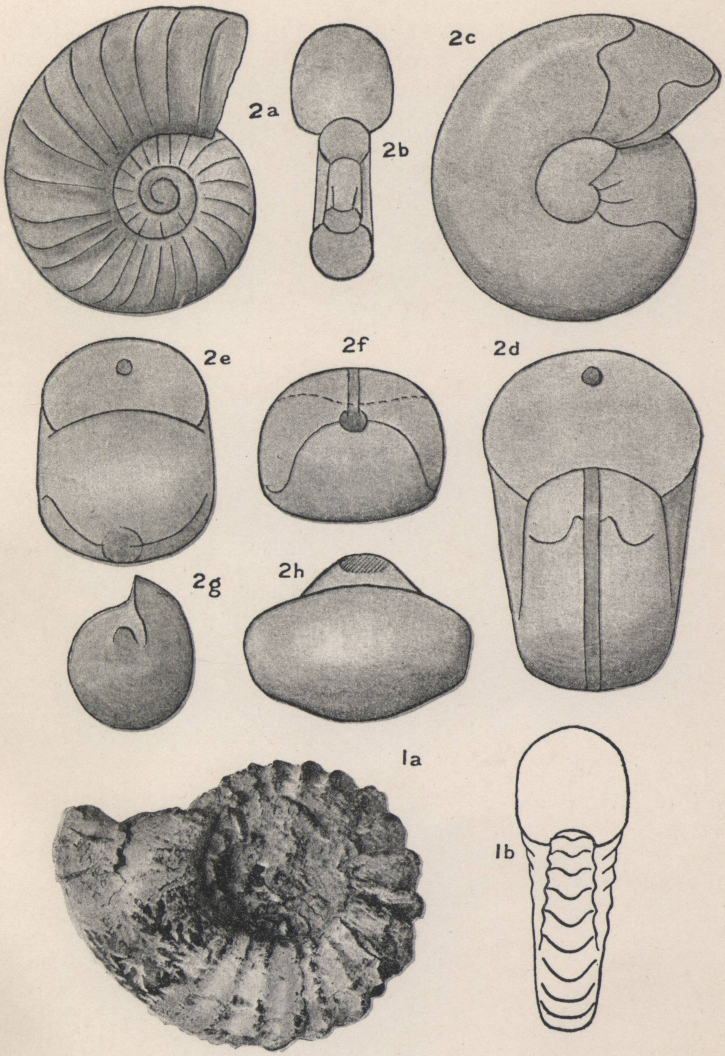
AMBLYCOCERAS, VICININODICERAS, CYMBITES.



A.E.T. del. et photo.

OISTOCERAS.

PLATE XXV.

Fig. 1. *Oistoceras allœotypum*, sp. nov. × ·52. From the lower beds of the *margaritatus* zone, Bracebridge Pit, Lincoln.

2. *Oistoceras omissum* Simpson. Development. From the *Oistoceras* sub-zone, Waddington, near Lincoln. *c*, *d* = Inner whorls × 32; *e*, *f* = Inner whorls × 37; *g*, *h* = Protoconch × 47.

DISCUSSION.

The PRESIDENT (Mr. G. W. LAMPLUGH) congratulated the Author on his lucid exposition of an intricate subject, and commented on the high importance, both to biologists and to stratigraphers, of intensive palæontological studies of this kind. He wished, at the same time, to call attention to the difficulties felt by the field-geologist, when robbed of his crude nomenclature of the commoner fossils by the precise definition and complicated analysis now attempted by the palæontologists. For general service some kind of name was essential, but was becoming increasingly difficult to acquire or retain. For example, it was most desirable to be able to express, as proof that certain beds were Upper Lias, that they yielded *Ammonites communis*, *bifrons*, and *serpentinus*, for every geologist would understand the statement. It might be based, quite soundly, on material so poor that no palæontologist could name the specimens, or so good that only a very small number of specialists in these particular forms would dare to do so. The growing difficulty would have to be met by some means, even if it entailed a duplication of nomenclature. We might have to continue to use indispensable names in a general sense, perhaps with some indication by type or symbol to warn the specialist.

The SECRETARY read the following communication from Mr. S. S. BUCKMAN:—

The title of this paper is a tribute to Alpheus Hyatt. It is just over 50 years ago that Hyatt published his remarkable scheme of Ammonite families and genera—a scheme so advanced for its time and so revolutionary that it found no acceptance in Europe for many long years. Here the later but far more modest scheme of Waagen held the field, yet even that was very strongly condemned as an undesirable innovation. I can remember in the 'seventies' the discussions of leading geologists and my father when they met at his table after their field excursions—the prophecies of disaster to palæontology, which would become quite distasteful to students from the multitude of new names. And now we see how these predictions have been falsified. A young student in almost his first paper takes one of Hyatt's original families, actually only a small portion of Waagen's genus *Ægoceras*, and finds it now divided into five genera, which he accepts. But in his critical analysis he discovers that these genera are insufficient: he promptly increases them by 80 per cent., admitting at the same time that many foreign species of the family must remain outside of them, so that the number of genera in this one family is not quite complete. Further, he shows his grasp of the subject by clearly stating the distinctions of the genera in a few words.

The family Liparoceratidæ is very interesting. In its geological distribution it illustrates the principle of faunal repetition alluded to in my last paper communicated to the Society. In its morphology, showing successive waves of

capricorns developing into bituberculate sphærocones, which may perhaps unduly hearten the protagonists of orthogenesis, it shows the difficulties that confront the field-geologist until a study like the Author's places facts in a clear light. In its biological development it illustrates the various phases of palingenesis which in 'Yorkshire Type Ammonites' I have called saltative, cunctative, precedentive. In the last, the hastening in development of one feature faster than another, we seem to have the clue to the origin of species—it makes for diversity of genera; while tachygenesis, or the earlier acquirement of characters, gives the differences of species. What was the cause of precedentive palingenesis touches the debatable ground between Weismannism and Neo-Lamarckism. I confess to a predilection for the latter—that the variations of the germ-plasm were not fortuitous, but, in some way, reflect modifications of the somatic cells induced by their responses to differences of environment. Data for solving this problem are required, and evolutionary studies such as those presented by the Author may be of great assistance.

Time forbids notice of many other interesting points in regard to the Liparoceratidæ, but one especially may call for remark. Again and again the genera reach the position of flourishing sphærocones, only to die out suddenly. By analogy with other Ammonite stocks there should have been a long period of catagenesis in front of them, passing to serpenticone stages again, with loss of ornament, and even with possibilities of renewed anagenesis. But nothing of this kind seems to happen—each stock appears to come to a dead end at the height of its career, or thereabouts; while the latest genus of all is the most flourishing sphærocone of the family.

In the Geological Table of his abstract the Author places *Beaniceras* as a capricorn, though, later, excluding it from the Liparoceratidæ. *Beaniceras* is a catagenetic capricorn following a unituberculate cadicone: the others are anagenetic capricorns. The family position of *Beaniceras* is doubtful. It occurs to me to ask where in the Liparoceratids is the unituberculate stage which in other Ammonite stocks precedes the bituberculate: do the massive ribs of capricorns really represent it? When he had nearly completed his investigations the Author showed me some of his interesting results, and, if I remember rightly, he had found in the ontogeny of some Liparoceratids traces of a temporary catagenetic capricorn condition. Now, it may be suggested that there is a non-sequence in the ontogeny of the capricorns (saltative palingenesis); that in the phylogeny there was a unituberculate cadicone stage which is omitted in the capricorn ontogeny, in the same way as the capricorn stage is omitted in the ontogeny of the sphærocones; and that *Beaniceras* is the genus which has preserved this unitubercular cadicone stage in its ontogeny, and shows it fading into capricorn. Is the temporary catagenetic capricorn condition a relic of this?

In conclusion, I congratulate the Author on an excellent piece of work. It is to be hoped that he will deal with other families in the same way, though in some (owing to mineral condition) suitable material is hard to come by, numerous though the specimens be.

Dr. A. M. Davies congratulated the Society and the Author on a first paper so valuable and so clearly set forth. He confined his comments to one aspect of the subject: What was the meaning of such developments as that from ribbed capricorn to tuberculate sphærocone, repeated time after time in the same stock? Was it adaptation to a changed environment? He found it difficult to believe this, and felt that we must here face a problem of evolution more fundamental than even that of Darwinism *versus* Lamarckism, both of which deal with adaptative evolution. He had been led to a conception of a varying 'margin of elasticity' between organism and environment. When this margin is narrow we have strictly adaptative evolution, as in the striking case of the

Mammalia; but, when it is wide, evolution may cease to be guided by environment, and orthogenesis may have free play. If change of environment narrows the margin, a possible result may be sudden extinction. The mode of life which appeared to afford the widest margin of elasticity was the microphagous; and he put forward as a speculation that the ammonites were not carnivores like modern cephalopods, but had reverted to the microphagous habit.

Prof. H. H. Swinnerton said that he had been in close touch with the Author while the work was being done, and could testify to the care with which the material had been collected. The Author had exercised due restraint in making new species; and, in the formation of new genera, had attempted to give them names descriptive of the ammonite, and therefore capable of being incorporated ultimately into a scientific nomenclature. He had been interested in the account of the way in which the capricorn stage was eliminated from development, and suggested that one factor in the process may have been the close similarity in general form between the globose early stage and the sphærocone late stage. He congratulated the Author upon the clearness with which he had set forth the subject-matter of his paper.

Dr. W. D. Lang suggested that the potentiality (demonstrated in this paper in the case of Liparoceratid Ammonites, and by other writers in various groups of animals), in primitive or radical forms for producing similar, definite, and progressively more complex structures in all its descendant lineages, should be distinguished from the Mendelian Factor, which, at first sight, it would appear to resemble. For example, it might be said that an evolute Liparoceratid carried the factor for involution; that, by the liberation of an inhibiting factor, the involution became actual. But, on the theory of the Mendelians, each such factor has a corresponding structural basis, so that the more (inhibited) factors are present, the more complex the structure of the nucleus that carries them. With potentiality, on the other hand, the simpler the organism is, the greater are its potentialities; and, though (as exemplified in Corals and Polyzoa, for example), the method of evolution often suggests that inhibitions are removed (perhaps by environmental changes affecting metabolism generally, and internal secretions in particular), whereby latent potentialities are liberated freely, as seen in wholesale outbursts or waves of evolution; yet, there is no reason to suppose that a potentiality is correlated with a definite structure. And, even in the case of the Mendelian Factor, such an assumption is in danger of ultimately leading to absurdity, if, as many Mendelians hold, a new character can only arise by the removal of an inhibiting factor: for the simplest organisms must then have the most complex nuclei—which, if not absurd, is at least improbable.

The Author, in reply to the President, pointed out that, while it was undesirable to use the names *Ammonites striatus* and *A. capricornus* with the wide meaning formerly given to them by stratigraphical workers, yet such terms as 'capricorn ammonite'

and '*striatus*-like ammonite' could be so used. He agreed with Mr. Buckman that there is little indication of the catagenetic changes which one would expect to follow the sphærocone stages; the beginning of catagenesis is shown, however, by a tendency to return to paired tubercles in some imparinode series. A unituberculate stage occurs in some series, and it did not seem necessary to him to suppose a *Beaniceras*-like ancestor representing this stage. Replying to Dr. Davies and Prof. Swinnerton, the Author said that the 'skipping' of the capricorn stage was accompanied by the omission of the slender-whorled stage, leading to the direct development of the involute form. He did not think that changes in the nature of deposits had any relation to changes in the form of the shell. In conclusion, he wished to thank the Fellows present for the kind reception accorded to his paper.

GENERAL INDEX

TO

THE QUARTERLY JOURNAL

AND

PROCEEDINGS OF THE GEOLOGICAL SOCIETY.

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